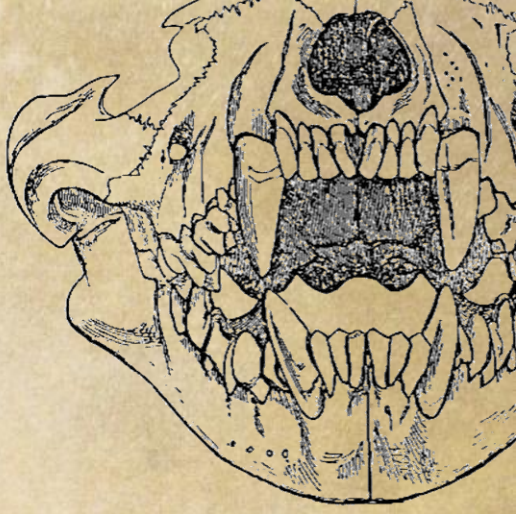


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THE SPATIAL EPIDEMIOLOGY OF THE DEVIL FACIAL TUMOUR DISEASE IN LONG-DISEASED POPULATIONS OF ITS UNIQUE HOST, THE TASMANIAN DEVIL

SEBASTIEN COMTE

BSc, MSc

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DECLARATIONS BY THE AUTHOR

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The research associated with this thesis abides by the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th edition, 2004 and the University of Tasmanian Animal Ethics Guidelines. The research presented in this thesis was carried out under University of Tasmania Animal Ethics Approval A13326 (2013-2016), A15835 (2016-19), the Tasmanian Department of Primary Industries, Parks, Water, and the Environment Permits TFA14228 (2015-2016), TFA16180 (2016-2017), TFA18028 (2018), TFA19004 (2019) and Forestry Tasmania Permit 1526 (2017).

I acknowledge and agree to the above stated declarations:

_____ 16/02/2019

Sebastien Comte Date

The following people and institutions contributed to the publication of research undertaken as part of this thesis:

Sebastien Comte: School of Natural Sciences, University of Tasmania (Candidate)

Menna Jones: School of Natural Sciences, University of Tasmania (Supervisor)

Rodrigo Hamede: School of Natural Sciences, University of Tasmania (Co-supervisor)

Scott Carver: School of Natural Sciences, University of Tasmania (Co-Supervisor)

Mark J. Margres: School of Biological Sciences, Washington State University, Pullman, Washington

Brendan Epstein: School of Biological Sciences, Washington State University, Pullman, Washington

Douglas H. Kerlin: School of Environment, Griffith University, Nathan, Queensland, Australia

Samantha Fox: Save the Tasmanian Devil Program, Department of Primary Industries, Parks, Water and Environment, Hobart, Tasmania, Australia

Alexandra K. Fraik: School of Biological Sciences, Washington State University, Pullman, Washington

Sarah A. Hendricks: Department of Biological Sciences, Institute for Bioinformatics and Evolutionary Studies, University of Idaho, Moscow, Idaho

Stewart Huxtable: Save the Tasmanian Devil Program, Department of Primary Industries, Parks, Water and Environment, Hobart, Tasmania, Australia

Shelly Lachish: Department of Zoology, University of Oxford, Oxford, UK

Billie Lazenby: Save the Tasmanian Devil Program, Department of Primary Industries, Parks, Water and Environment, Hobart, Tasmania, Australia

Sean M. O'Rourke: Department of Animal Science, University of California, Davis, Davis, California

Amanda R. Stahlke: Department of Biological Sciences, Institute for Bioinformatics and Evolutionary Studies, University of Idaho, Moscow, Idaho

Cody G. Wiench: Department of Biological Sciences, Institute for Bioinformatics and Evolutionary Studies, University of Idaho, Moscow, Idaho

Barbara Schönfeld: School of Natural Sciences, University of Tasmania, Hobart, Tasmania

Hamish McCallum: School of Environment, Griffith University, Nathan, Queensland, Australia

Michael R. Miller: Department of Animal Science, University of California, Davis, Davis, California

Paul A. Hohenlohe: Department of Biological Sciences, Institute for Bioinformatics and Evolutionary Studies, University of Idaho, Moscow, Idaho

Andrew Storfer: School of Biological Sciences, Washington State University, Pullman, Washington

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Contributions: SeC and MJ designed the study and managed the data acquisition. SeC analysed the data with the help of MJ, SC and RH. SeC drafted the manuscript and all authors provided feedback and gave final approval for publication.

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We, the undersigned, agree with the above stated proportion of work undertaken for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

_____

Menna Jones
Candidate's supervisor
School of Natural Sciences
University of Tasmania
Date: 15/02/2019

_____

Greg Jordan
Head of Discipline
School of Natural Sciences
University of Tasmania
Date: 16/02/2019

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"Ce que nous pouvons faire de mieux au monde, c'est être heureux, faire le bien et laisser piailler les moineaux"

Don Bosco

III. ABSTRACT

Emerging infectious diseases in wildlife are recognized as a major conservation threat, globally. Their impact is rarely as acute as the novel transmissible cancer, devil facial tumour disease (DFTD), on its unique host species, the Tasmanian devil (Sarcophilus harrisii). Since discovery in 1996, the disease has caused overall population declines of 77%, with local declines in excess of 90%. While localized extinction has not been documented, much of Tasmanian landscapes are functionally depleted of the largest carnivore. There are encouraging signs of tolerance and resistance emerging in wild populations, but these have not yet resulted in measurable, sustained recovery. This thesis proposes a multiscale framework to understand the effect of the cancer on the spatial ecology and movement ecology of Tasmanian devils with potential repercussion on transmission of DFTD in long-diseased areas of the north-east Tasmania.

The research presented here is the result of intensive fieldwork from 2015 to 2018, building on long-term datasets since 1999, bringing deeper knowledge on demography and spatial ecology of Tasmanian devils, from daily movements to large-scale distribution. In 2015 and 2016, GPS tracking devices were fitted to adult devils in the Freycinet Peninsula, including animals presenting clinical signs of DFTD. Previous tracking data (using VHF radiotracking technology) gathered in the Freycinet peninsula in 2001, allowed the comparison of spatial organization before and after the outbreak. In 2017, a large-scale (2900 km^2) camera trap survey was implemented in the north-east Tasmania to predict the abundance distribution of devils in the long-diseased areas. Additionally, as part of a long-term monitoring program, live trap surveys were conducted every year in two coastal populations, wukalina (30 km^2) and Freycinet (300 km^2). These surveys were used to challenge the large-scale spatial distribution when down-scaling and up-scaling the empirical survey.

In Freycinet, DFTD infection was associated with a decrease in daily movement activity with males showing a stronger response than females. At the population level, after controlling for differences in tracking technologies (VHF vs GPS), the reduction in devil density in Freycinet resulted in smaller home range sizes for females and a more clustered spatial organization, a trend not observed for males. At a larger spatial scale in the north-east of Tasmania, abundance distribution was strongly influenced by the design of the empirical survey and the spatial scale at which the effect of the habitat was measured. Distribution and abundance of devils was predominantly driven by the presence of low cover (heathland and scrub) and forest cover, while rugged landscape was negatively selected. The predicted distribution in the north-east was heterogenous with hot spots in coastal areas, interconnected with low altitude dry sclerophyll forests. High altitude wet forest and large open areas were the least suitable habitat in these long diseased populations.

Collectively, this research indicates that the DFTD outbreak influenced the spatial and movement ecology of Tasmanian devils at different scales. This likely resulted in lower contact rates and less competition for resources. Less aggressive behaviours in the population could in turn reduce disease transmission. The heterogenous abundance distribution of devils suggests that meta-population mechanisms could underlie the current epidemiology of DFTD where local extinction and colonization may increase the resilience of the host species at landscape scales. Additionally, the results suggest that females are more important for the local persistence of the disease.

This research provides new insight on how pathogens directly and indirectly influence the spatial ecology and movements of their hosts. The study of these relationships at different spatial scales opens new perspectives to understand host persistence to infectious diseases. This research supports and encourages the future development of spatial epidemiology for wildlife diseases to better inform conservation strategies.

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1.1. Context for the thesis: A brief history of research on the Tasmanian devil and DFTD

Tasmanian devils (*Sarcophilus harrisii*) are the largest extant carnivorous marsupial (Family Dasyuridae) and are endemic to the island of Tasmania. Devil populations have shown major demographic variations since European settlement (Guiler, 1970b, a, 1982; Bradshow and Brook, 2005). With a growing human activity in the second half of the 1800's, leading to land clearance for pasture, devils were considered as a threat for the livestock industry and a bounty was offered for each animal killed. Populations decreased drastically until they were eventually legally protected in 1941 (DPIPWE, 2010). During the second half of the century, devil populations recovered, benefitting from land clearance and macropod culling (more carrions available) (Guiler, 1978). Present over the whole island of Tasmania (Jones and Barmuta, 2000), devil density reached its highest recorded in the early 1990's (Owen and Pemberton, 2005) with populations close to local carrying capacity of the habitats (Lachish et al., 2007).

In 1996, a devil was photographed in the north-east of Tasmania, with large skin lesions and what seemed to be excrescences (Hawkins et al., 2006). Based on samples collected from 2003 onwards, these were identified as a new infectious disease caused by the transmission of live tumour cells resulting in large tumours growing on the face of devils (Loh et al., 2006; Pearse and Swift, 2006). Because the disease was new, the first decade saw the research effort following three main directions. The first five years were focussed on understanding the population effects of the disease and its epidemiology. A decision tree was developed early on to guide priorities for research and action for new and emerging infectious diseases, about which little is known, and using the Tasmanian devil – DFTD and frog – chytrid host-pathogen systems as examples (McCallum and Jones, 2006). This led to the first and emergency management action of establishing insurance populations isolated from the disease, in case of extinction and the need to reintroduce devils to their former range in Tasmania (McCallum and Jones, 2006). Wild devil populations were monitored using live trapping to assess the effect of the DFTD on the fitness and life history of the hosts. This research has shown radical changes in the age structure of devils, a reduction in female dispersal, earlier primiparity for females and larger litter sizes (Lachish et al., 2007; Jones et al., 2008; Lachish et al., 2009). In parallel, strong efforts were made to describe the

epidemiology of the novel cancer, which showed a mostly frequency-dependent transmission route by direct contact between individuals with high potential to drive the host population to extinction (McCallum and Jones, 2006; McCallum et al., 2007; Hamede et al., 2008; McCallum et al., 2009). Further management measures were then explored: culling of infected hosts (Lachish et al., 2010), monitoring of wild populations for potential natural evolution of the host-pathogen system, and developing preventive or curative treatment (Jones et al., 2004; Jones et al., 2005; McCallum and Jones, 2006; Jones et al., 2007; Siddle et al., 2007; Woods et al., 2007)

During the next decade, large efforts were made to understand the origin and aetiology of DFTD (Murchison et al., 2010; Murchison et al., 2012; Pye et al., 2016), providing crucial knowledge to study the physiological impact of DFTD on devil fitness and to further the research on potential prophylactic tools. The laboratory work was strongly facilitated by the growing collection of tissue samples collected during the ongoing longitudinal monitoring of wild devil populations across the species range (Hamede et al., 2012). Seasonal monitoring created the baseline to develop the first epidemiological models (SEIR model), initially predicting the likely extinction of devils in a foreseeable future (Beeton and McCallum, 2011; McCallum, 2012). A high priority identified early on (McCallum and Jones, 2006) was the potential cascading effects of the loss of Tasmania's largest carnivore on the trophic network, triggering further extinctions or declines of small biodiversity. Analysis of long-term wildlife monitoring using spotlight surveys across the whole island of Tasmania, started before the emergence of DFTD, and a space-for-time study across the entire east-west range of disease outbreak times using hair traps, suggested that the spread of DFTD had induced the meso-predator release of feral cats in the long diseased areas (Hollings et al., 2014; Hollings et al., 2016). This study also highlighted the potential for the trophic cascade to lead to a disease cascade via increased transmission of *Toxoplasma gondii* to wildlife and livestock from its sole host, the feral cat.

Sustaining and even increasing the regular monitoring of populations across Tasmania has now created a rare dataset covering most of the species range (Lazenby et al., 2018), with individual life histories spanning from before the emergence of DFTD to almost 20 years post outbreak and still going (Lachish et al., 2007; Hamede et al., 2012). With a large collection of biological tissue samples from host devils and matching host tumours from multiple sites, that commenced in 1999 prior to disease outbreak (M. Jones pers. comm.), it has been possible to document the emergence of rapid evolution of host resistance and tolerance to the disease (Margres et al., 2018b; Ruiz-Aravena et al., 2018a). Being able to link these genetic studies with the natural history of the devil populations has allowed for more complex epidemiological models and revising of the early prediction of devil extinction with support for long term co-existence of devils and DFTD (Wells et al., 2017; Wells et al., 2018). This has led to management advice of the importance of conserving adaptive potential in the devil and avoiding management that may compromise this (Hohenlohe et al., 2019). Even though the ecology of the devil has been reasonably well documented, there was a knowledge gap on the spatial component of devil natural history, especially in relation to the transmission of DFTD. It is this gap that the thesis addresses.

1.2.Mapping the disease

Spatial sciences and epidemiology are fundamentally linked through the concepts of place and neighbourhood, forming the discipline of spatial epidemiology (Kirby et al., 2017). This field of research, mainly focused on human epidemiology, relies on spatially referencing disease cases (place) to analyse their pattern of distribution (neighbourhood) in relation to intrinsic (patient's sex, age, socio-economic background, etc.) and extrinsic (exposure to pollutants, proximity to health services, etc.) risk factors (Roquette et al., 2017). These maps are generally created *a posteriori*, using all available information to identify potential factors linked with a particular disease outbreak, like the epidemic of severe acute respiratory syndrome (SARS) in Beijing in 2003 (Wang et al., 2006). They can also be used to predict the risk of outbreaks in changing environmental conditions such as the effect of El Nino oscillations on the probability of Rift Valley fever outbreaks in the Horn of Africa (Anyamba et al., 2009).

A very similar framework in ecology, globally referred to as species distribution models (SDM), is used to measure and predict species occurrence and abundance in space and time (Acevedo et al., 2017). Where the background mapping of the neighbourhood is identical to spatial epidemiology, the concept of place differs substantially for wildlife, the closest concept would be that of the ecological niche (Holt, 2009). Unfortunately, heterogeneity of data on species' niches is usually a limiting factor, especially when precise estimation of occurrence or densities are needed. In these cases, specific surveys must be implemented with repeated standardized observations of a subsample of the population (Steenweg et al., 2018), while accounting for imperfect detection. Occupancy models are one of the major statistical tools used to estimate local occurrence (Royle et al., 2005) or abundance often predicted by habitat or bioclimatic covariates. In the last two decades, methods to observe species in the landscape have evolved from intrusive and labour-intensive live trapping protocols to passive remote sampling using camera traps and remote DNA collection (Burton et al., 2015). With these new tools, it is possible to cover larger areas and to more feasibly survey cryptic species generally expanding innovation in SDM.

To map wildlife diseases, one must combine the concepts of spatial epidemiology and SDMs to correlate the distribution of the host species with risks factors associated with the pathogen eco-epidemiology. Widely used to map the risk of exposure to vector borne diseases, like cutaneous leishmaniasis (Chalghaf et al., 2016) or Lyme disease (Guerra et al., 2002), these maps can also reveal or predict the spatial spread of pathogens over time (Combes et al., 2012) and consolidate the design of targeted prophylactic measures (Blanton et al., 2006).

The future challenge for disease mapping, however, is the inclusion of multiscale frameworks to better account for the heterogeneity in host distribution and its implication for pathogen spread. There is increasing empirical evidence that model outputs of wildlife distributions are dependent on the scale at which data are collected (Holbrook et al., 2017; Bhakti et al., 2018). Similarly, the scale at which disease cases are aggregated can influence the relative importance of covariates in predicting disease exposure (for example, Ross River Virus, Flies et al. 2017). Finally, many epidemiological studies are bound to administrative units which do not always match the epidemiological processes underlying wildlife diseases emergence and spread (Riley et al., 2015).

1.3.Monitoring host populations

Classically, epidemiological models interpret the host-pathogen system by compartmenting the host population into discrete epidemiological states such as susceptible (S), exposed (E), infected (I) and recovered (R) (Oli et al., 2006; Vyska et al., 2016). By comparing the intrinsic characteristics of these different groups, it is possible to identify and classify the main risk factors associated with a pathogen infection and to measure the prevalence of the disease in the population. Repeating the process over time gives a measure of the force of infection (Hens et al., 2009), the incidence of a disease and the basic reproductive number (R_0) (Diekmann et al., 1990); which are three fundamental metrics of the transmission rate of a pathogen. The mechanistic combination of these epidemiological concepts and the population dynamics processes of birth rate, ageing and mortality rate, commonly incorporated into to as SEIR models, has transposed the descriptive field of epidemiology into a predictive framework. Over time, epidemiological models have been advanced through inclusion of individual heterogeneity of traits and responses (Warburton and Vonhof, 2018). Efforts are also being made to embrace the role of co-infection in host-pathogen systems (Sofonea et al., 2015) as well as the role of biodiversity in disease transmission (Dobson and Auld, 2016). All of these models, despite their increasing complexity, still strongly depend on the detection of the pathogen and the estimation of the host population density (Cooch et al., 2012).

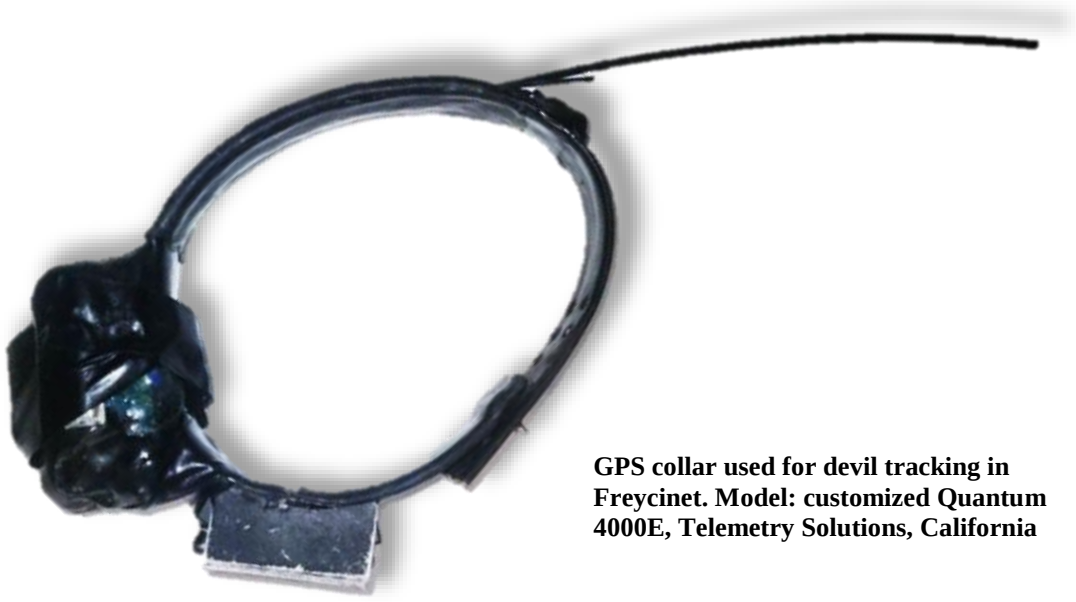
Because most pathogens are microscopic and often hidden within their host, it is very difficult to directly observe their distribution without accessing the host. Humans with their domestic animals usually consult their physician and veterinarian and the latter can also access livestock on farms. Access to wildlife, on the other hand, is much more difficult. Post-mortem analyses of dead animals (derived from roadkill, hunting and obtained via citizen science) can be valuable survey methods but they are often not representative of the whole host population (Lawson et al., 2015). Faecal collection is increasingly used to detect pathogen infections (Henry et al., 2018; Knapp et al., 2018). In many cases, though, the only way to diagnose an infection is to collect blood, urine or tissue samples directly from the host species by attracting them into traps. Live trapping enables individual identification (tagging, marking, DNA sampling), and measurement of fitness and life history traits (growth, reproduction, survival, age at first breeding) which sum to population dynamics processes. This information can then be used to inform SEIR models (Mariën et al., 2018).

Capture-recapture protocols and statistical analyses have a long history in ecology (Nichols, 1992) and are still widely used today (Henle and Gruber, 2018). The last decade has seen the emergence of a new type of capture-recapture model with the inclusion of spatial data. The main contribution of these models is to directly estimate the density of a species without having to arbitrarily define the effective trapping area (Borchers and Efford, 2008; Royle et al., 2018). Because the detection probability at each capture is modelled as a function of the distance to the theoretical activity centre of the individual (Efford et al., 2009), it is possible to infer home range sizes and spatial organization of the population (Efford et al., 2016). The use of spatially-explicit capture-recapture (SECR) models in epidemiology is still marginal, but represents a strong potential to further our understanding of the effect of density and spatial organisation on pathogen exposure, prevalence and transmission (Christiansen et al., 2015; Muneza et al., 2017)

Female Tasmanian devil fitted with a proximity logger. © Sebastien Comte

1.4.Tracking the individual host

Probably the most flourishing field of spatial ecology in the last twenty years, animal tracking is still neglected in epidemiological studies. Organisms inhabit heterogenous landscapes in which resources are patchily distributed in space and time. Tracking devices have been extensively used to measure the association of habitat and animal activity (Kays et al., 2015), with the classical approach of calculating the home range of the organism as the area necessary to meet all its needs (Burt, 1943; Worton, 1987). It is then possible to quantify the utilization distribution of the animal as its probability to be at a given location which can then be matched with habitat or resource maps, commonly named the resource selection function (Boyce et al., 2002; Seidel and Boyce, 2016). When multiple animals are tracked at the same time in the same area, it is possible to compare their home ranges (relative size and location), an approach widely used to describe the spatial and social organisation of a species in contrasting landscapes (Mäkeläinen et al., 2016). With the increasing use of Global Positioning System (GPS) tracking devices, researchers have unprecedented access to animal movement (Kuenzer et al., 2014). Trackers as small as 5 g can record the location of animals multiple times per minute (Santos et al., 2019) and record the animal's activity using accelerometers (Willoughby, 2017). We can now follow the movement decisions of individuals based on available resources and competition and measure their plasticity in movement when these conditions change (Hernández-Pliego et al., 2017).



GPS collar used for devil tracking in Freycinet. Model: customized Quantum 4000E, Telemetry Solutions, California

The fitness of infectious pathogens depends on their capacity to move or transfer their offspring from one host to the other. Understanding the spatial organisation of the host species is therefore essential to predicting the emergence and spread of a pathogen. Resnik et al. (2018) showed that island fox (*Urocyon littoralis*) home ranges were significantly larger near roads and that these foxes were moving longer distances, creating preferential corridors for the spread of pathogens. Home range overlap has direct influence on the contact rate between individuals and therefore impact on the transmission of pathogens (Vander Wal et al., 2014). In addition, infectious diseases alter physical, physiological and behavioural traits of their host ecology (Rosatte et al., 2006; Marco et al., 2009), which directly or indirectly influence the spatial organisation of the population (Sah et al., 2017). A common individual response to infection is to develop sickness behaviours. This concept refers to adaptive changes in behavioural patterns related to the physiological costs associated with a disease (Lopes, 2014). Sickness behaviour often results in lethargy, somnolence or anorexia, all behaviours that could be measured with current tracking devices.

GPS tracking devices are now used on livestock and even humans with the potential to inform on exposure to pathogens (Bailey et al., 2018; Kestens et al., 2018). Unfortunately, as for everything, animal tracking has its down side. The costs of GPS tracking devices are still expensive (but quickly reducing), which often limits the number of individuals in the samples. In some cases, when the duration of the study is longer than a year or the frequency of the locations is high (less than 1 hour between fixes), GPS tracking becomes less costly than VHF tracking, especially due to the high human costs of the latter (Recio et al., 2011). Even if the collars are getting smaller, they may still have a direct impact on the individual animal's behaviour and fitness (Walker et al., 2011), especially for diseased animals already weakened by the pathogen infection. Constant monitoring of the animals is recommended, which can be tedious and time consuming. These costs can be reduced by data sharing through online data repositories and collaborative studies.

1.5. Thesis aim and outline

In my thesis, I explore the role of spatial ecology and movement behaviours of devils in the persistence of DFTD in the long diseased areas of the north-east Tasmania. I present a multiscale framework adapted from the concept of resource selection order introduced by Johnson (1980) and still central to ecological research today (Reiners et al., 2017; McCallen et al., 2019). I use a three-level framework: the species distribution, the placement of individual home ranges in the landscape and the individual movement decisions within the home range.

In chapter two, I draw the spatial distribution of Tasmanian devils in the long diseased area of the north-east of Tasmania. I first test the effect of heterogeneity in topography and vegetation cover on the large scale (3000 km^2) abundance distribution of devils while accounting for the specific scale of influence of the covariates. I then challenge the large-scale prediction based on camera traps with two live trapping surveys on smaller study areas, 300 km^2 and 30 km^2. This chapter will provide the first regional map of distribution of abundance for the endangered Tasmanian devil, a necessary tool to design efficient management strategies. My results will also contribute to understanding the spatial spread of DFTD and its long-term persistence while empirically measuring the effect of the spatial scale of species distribution models.

In chapter three, I measure the plasticity in spatial organisation in a Tasmanian devil population before and after the outbreak of DFTD. I first assess the magnitude of the decrease in density using spatial explicit capture recapture based on live trapping monitoring. I then compare the home range sizes and overlap using tracking data from before the outbreak of DFTD and fifteen years later. Changes in spatial organisation likely influence the contact rate between individuals with direct consequences for the transmission of the disease. The observation from the devil-DFTD system and the method used to match different tracking technologies can be transposed in many wildlife host-pathogen systems for which pre-disease data are sparse or not available.

Chapter four focusses on the direct impact of cancer on the movement of individual host. Here, I hypothesise that the metabolic cost of tumours influences the movement decisions of devils at different spatio-temporal scales, from seasonal home range to single to fifteen minutes steps. I present the first fine-scale GPS tracking of devils with clinical signs of DFTD and compare their movement decisions to healthy animals tracked at the same time in the same population. I then project my finding in the context of a DFTD outbreak in a naïve population using tracking data from north-west Tasmania. My results will inform the capacity of devils to adapt their movement behaviour when infected, with implications for the local persistence and transmission of DFTD.

Finally, in chapter five, I discuss the importance and benefits of using a multiscale framework to integrate spatial ecology and movement ecology in epidemiological studies. I first synthetize my findings at each scale and discuss their significance in revealing across scale epidemiological processes. I then reflect on the potential benefit and limit of this approach for different host-pathogen systems and identify the future challenges of wildlife epidemiology.

Male Tasmanian devil in Freycinet. © Sebastien Comte

1.6.References

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CHAPTER 2: Scale affects predictions of the distribution of abundance in an endangered species: long-diseased populations of the Tasmanian devil.

J.R.R. Tolkien

2.1. Introduction

Despite recognition of the fundamental importance of abundance and occurrence in ecological theory (Krebs, 1972) and conservation practice (Gaston, 1997; Guisan et al., 2013; Martin et al., 2018), limited resources frequently restricts acquisition of data to spatial scales that do not always match the scale of ecological processes under investigation (Hiers et al., 2016; Kukkala et al., 2016). While recent technological developments provide more affordable survey methods (e.g. remote cameras, satellite imagery, DNA collection), data on species distribution remain highly heterogenous (Morán-Ordóñez et al., 2017), especially for cryptic and wide-ranging species. Contemporary analytical tools provide methods that have the potential to up-scale predictions from local, patchy information to larger areas (Peterson and Soberón, 2012), as well as down-scaling broad datasets to local patterns (Kunin, 1998; Groom et al., 2018). The amplitude and direction of the mechanisms driving the distribution of a species may vary with the geographic scale at which they are observed (Godsoe et al., 2017), however, a concept that is understudied and may be often be underestimated.

The accuracy and relevance of species distribution models (SDM) strongly depends on the quality and complexity of the empirical observations of the species of interest. The basic approach, using presence data only within a generalized linear model (GLM) framework (Peterson and Soberón, 2012; Franklin, 2013), is used widely to infer threats to global biodiversity, such as climate change or habitat degradation (Guisan and Zimmermann, 2000). These simplistic models can be greatly improved by accounting for absence data and imperfect detection (Lahoz-Monfort et al., 2014). Additionally, occupancy models, which rely on spatio-temporal replicates of presence/absence surveys (Bayley and Peterson, 2001; MacKenzie et al., 2002), are increasingly being used to describe habitat suitability and conservation threats at the species level (Thorn et al., 2009; Holbrook et al., 2017; Linden et al., 2017). When individuals in a population can be identified (e.g. by using natural markings or human-placed tags), it is possible to add the count of individuals detected into the occupancy framework, thereby accounting for heterogeneity in detection probability due to local abundance (Royle and Nichols, 2003; Kéry et al., 2005). This extra layer of information is crucial when monitoring very mobile species with large home ranges (Latham et al., 2014; Latif et al., 2018), for which occupancy alone could underestimate the heterogeneity in abundance of spatial distribution (Gaston and Fuller, 2009; Guélat and Kéry, 2018).

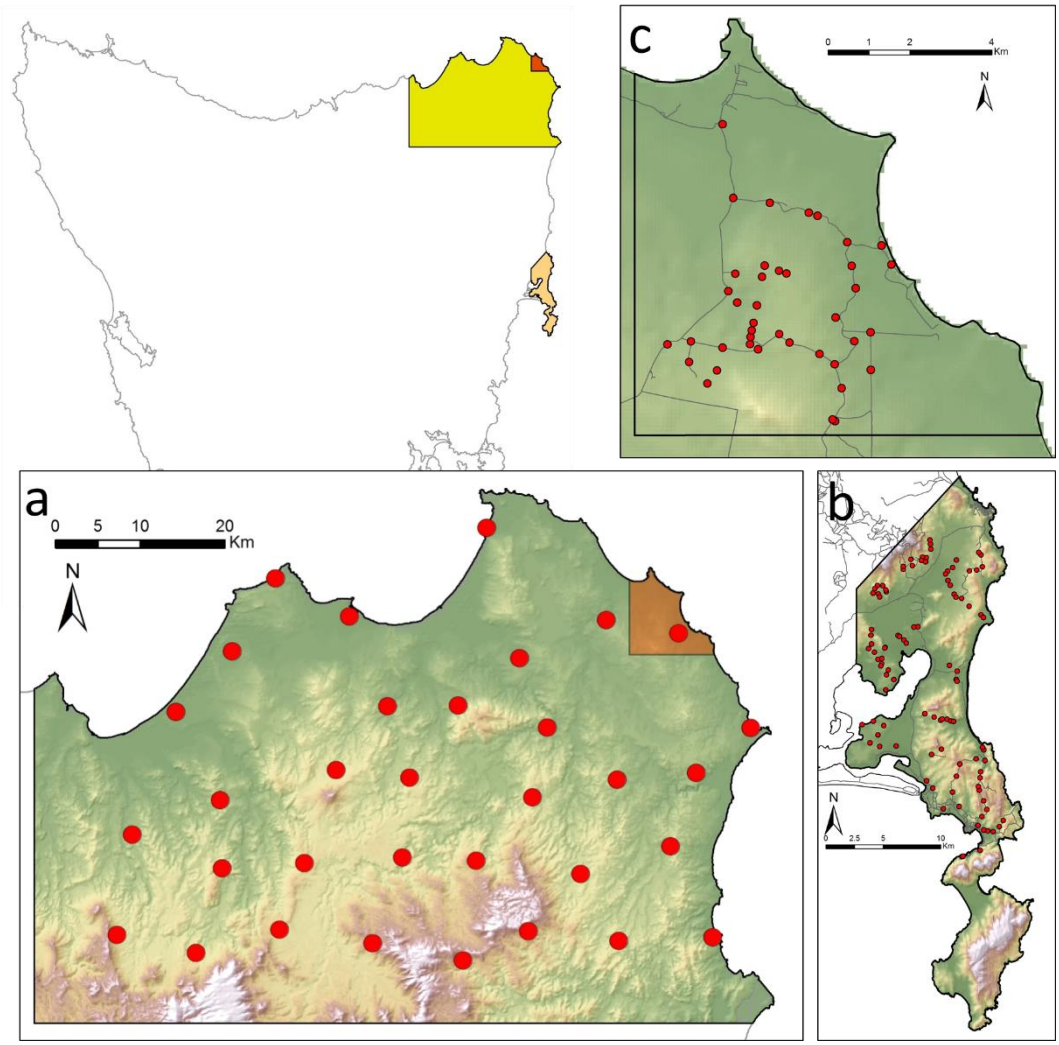
The relationship of abundance or occurrence of a species to the biotic and abiotic characteristics of a given landscape should integrate the spatial scale of both the species perception of the landscape and the organisational level of the survey. From the animal perspective, different habitat features may have differential spatial importance depending on the scale of movement activity. Different scales of movement and their ecological relevance include: proximal or immediate movement, local environment for daily resources, home range fulfilling all individual needs, and larger scale considering inter-individual connectivity. The organisational level (from individual to population to species range) at which the survey method is implemented can directly influence the effect of habitat covariates on the predicted distribution, hence the increasing development of multiscale models (Romero et al., 2016; Bhakti et al., 2018). This higher complexity of distribution models comes with stronger requirements for the empirical data used as input (Guillera-Arroita et al., 2015). Designing and implementing specific protocols that take into account every scale is not always possible and most conservation studies and management policies must rely on existing datasets often at a single organisational level.

In the last twenty years, populations of the largest extant marsupial carnivore, the Tasmanian devil (*Sarcophilus harrisii*), have declined severely across almost their entire distributional range on the island of Tasmania, Australia, due to the spread of a novel transmissible cancer (Hawkins et al., 2006; McCallum et al., 2007). The distribution of this endangered species is poorly understood, particularly in areas of severe population decline. Once widespread and locally abundant (Guiler, 1982), the spread of devil facial tumour disease (DFTD) since 1996 has resulted in an average decrease in density of 77% (Lazenby et al., 2018) and local losses of more than 90% of the population (Hawkins et al., 2006; McCallum et al., 2007). Most of the effort for the monitoring of devils is spatially patchy, concentrated in small trapping sites (usually 5 km by 5 km), with an even smaller number of temporally intensive monitoring sites.

The Tasmanian devil - DFTD study system, with its detailed local monitoring data and widespread, severe reduction in density, provides an excellent opportunity to assess fundamental questions in the role of spatial scale in assessing species distribution models for conservation purposes. We ask the following questions, using devils as a case study. (1) Is there an effect of spatial scale in how landscape features are perceived to influence the distribution of abundance? For this question, we conduct analyses of habitat associations at

multiple spatial scales using data from a broad-scale camera survey in the longest diseased area in north-east Tasmania where devil populations have been severely depressed for almost 20 years. (2) Is there benefit in using abundance in spatial distribution models, compared to occupancy models based on presence and absence data? For this question, we evaluate models built using abundance and presence—absence data over the same large-scale area. (3) Can landscape-scale spatial occupancy predict smaller scale distribution (down-scaling) and can small scale occupancy predict large scale distribution (up-scaling)? To answer this question, we use two additional live-trapping datasets, collected at small scale, in addition to the large-scale camera trap survey.

Figure 1: Maps of the study areas and location of the sampling stations (red spots). a) North-east Tasmania, 2900 km^2, 33 sampling stations with two camera traps for 21 days. b) Freycinet area, 300 km^2, 108 live traps for seven days. c) wukalina area, 30 km^2, 40 traps for ten days.



2.2.Materials and methods

2.2.1. Large scale abundance distribution in north-east Tasmania

The study area covers 2,900 km^2 of the far north-east corner of Tasmania, bordered by Bass Strait to the north and the Tasman sea to the east. The coastal areas of the north-east comprise extensive flat plains at low altitude, while the south western half of the area has a strong altitudinal gradient to 1122 m at Mount Maurice. The vegetation changes from coastal heathland and livestock pasture on the coastal plain (mean annual rainfall: 490-1050 mm), to native dry eucalypt forest and plantations at lower altitudes, and wet eucalypt forest and some rainforest at higher altitudes and in deep gullies (mean annual rainfall: 798-1900 mm).

Between February and March 2017, we conducted a camera survey, with camera stations spread across all vegetation communities in the study area, from the coast to the highest altitude. We set up 33 survey stations (Figure 1a) with two opposing camera traps (Reconyx PC800) pointing to a central bait canister filled with fish oil, attached to a visual lure (hanging compact disk) to maximize the detection of carnivores. The survey stations were at least ten kilometres apart to ensure spatial independence (O'Connell and Bailey, 2011), based on available home range data for devils (Thalmann et al., 2016; Andersen et al., 2017b). The cameras were set for 21 nights with the baits refreshed and the images downloaded on day 7 and day 14, creating three temporal replicates for each station. Individual devils were identified from their variable patterns of white marking on the chest, shoulder or rump against a black coat. Considering the low density, these markings were sufficiently unique to allow a count of the number of different individuals visiting each station during each seven-nights replicate (maximum of five individuals).

We characterized the habitat into three covariates describing the major structures of the landscape. First, using the existing digital elevation model for Tasmania (Land Information System Tasmania, https://www.thelist.tas.gov.au), we created a raster layer of the Terrain Ruggedness Index (TRI, Riley et al., 1999) a continuous variable with a value assigned for each 100 m x 100 m grid cell. Using the same grid, we recorded the presence on each cell of both low cover, such as heathland or scrub, and forest cover (0 = no, 1 = yes). To determine the scale at which habitat covariates affect devil abundance, we assigned to each grid cell the arithmetic average value over an increasing circular buffer, ranging from a scale that reflects proximal habitat use (500m radius from the camera site), daily movements

(1000m radius), home range (3000m radius) to a scale twice the size of a large home range (5000m). For each sampling station, we extracted the value for each covariate as the value of the cell containing the GPS location of the camera traps.

We used the replicated counts of individuals at each station to fit an N-mixture model (Royle, 2004) to test the effect of the covariates on devil abundance. We considered 64 candidate models representing all possible combination of the three covariates (TRI, low cover, forest cover) at each scale (500m, 1000, 3000m, 5000m). As we used the same model of camera and the same bait for each station, we kept the probability of detection constant across all sites while allowing for differences between temporal replicates (1 to 3). We used a Poisson distribution for the mixture estimator as the data were generally low value counts, and Poisson distribution provides more ecologically reasonable predictions for these kinds of abundance data (Joseph et al., 2009). Prior to fitting the models, all covariates were standardized using the function "scale" of the package "base" in R (2017, version 3.3.3). For the final model, we selected the buffer radius for each covariate that had the highest AICc weight (Burnham and Anderson, 2002). All models were fitted using the function "pcount" in the package "unmarked" in R.

We then spatially predicted the final abundance distribution over the whole area using the R function "predict" from the package "unmarked" on the covariate raster layers using the mean and standard deviation from each covariate standardization. Spatial mapping was done with the software ArcGIS (version 10.2.0.2248).

2.2.2. Does abundance improve occupancy predictions?

Standard occupancy models rely on presence/absence data with spatial and temporal replicates. To calculate occupancy, we used just the presence (1) or absence (0) of the species during the three consecutive replicates of seven nights, instead of counting the number of individuals photographed by the camera traps. We could then fit a single season occupancy model (MacKenzie et al., 2002) with the same framework as the N-mixture model for abundance. We allowed the detection probability to vary between the replicates but not between the sampling stations and used the same covariates for the occupancy as the final abundance model. We then spatially predicted the probability of occupancy over the whole area using the covariates rasters.

To compare the two species distribution models (abundance vs occupancy), we used a Spearman's rank test of correlation (Best and Roberts, 1975) between the two predicted maps. High correlation corresponds to values of *rho* close to one, while low correlation result in values close to zero.

2.2.3. Up-scaling and down-scaling the occupancy predictions

To test the robustness of the spatial prediction when changing the scale of the empirical data used as input, we considered the previously described camera trap survey (2900 km^2) and two live trapping surveys over smaller areas (Figure 1b+c): Freycinet (300 km^2) and wukalina (30 km^2). The Freycinet Peninsula on the east coast of Tasmania is approximately 30km long and averages about 5km in width. Most of the peninsula is steep and rugged, with sandstone and granite mountains (up to 620 m). Predominant vegetation is dry eucalypt forest, with a mosaic of heathland, scrub and native grassland at lower altitudes. The mainland connection to the northwest has large patches of open pasture supporting sheep and cattle farming. The second study area is situated at the northern tip of the wukalina/Mt William National Park, enclosed in the larger area covered by the north-east camera trap survey. Bordered by the Tasman sea on the north and east, the area presents a low topographical profile with the only relief being Mt William (216 m) in the south. On the coast, continuous white sand beaches are bordered by a dry heathland complex. Further inland, the vegetation becomes a mosaic of open grassland, maintained by the intense grazing of macropods, low scrub vegetation and dry eucalypt forests.

Both sites are part of state-wide annual monitoring of Tasmanian devil populations using live traps (long PVC pipes) baited with meat. In Freycinet, 108 traps were deployed (three trap lines) for seven continuous nights in December 2016. In November 2016, wukalina was surveyed with 40 traps, evenly distributed, set for ten continuous nights. During both surveys, the traps were checked every morning and missing bait replaced. The model of trap allowed for only one capture event per night with no release, preventing any animal from being captured in two different traps. Each animal trapped being microchipped, we could certify that any devil was only caught once per night. We then used each night as a temporal replicate, with presence (1) or absence (0) of devil, to fit the same occupancy model used for the camera trap survey with both datasets (Freycinet and wukalina).

At each spatial scale (north-east, Freycinet, wukalina), we predicted the occupancy distribution using the model outputs from the matching dataset. We then down-scaled the distribution model of the northeast region by using the north-east model covariates to predict occupancy at Freycinet and wukalina. Similarly, the distribution model for Freycinet was up-scaled to the north-east region and down-scaled to wukalina, and the distribution model for wukalina was up-scaled to Freycinet and to the north-east area. We compared the up-scaled and down-scaled predictions with the reference distribution map at each scale, using a Spearman's rank test of correlation performed in R.

2.3. Results

2.3.1. Large scale abundance distribution in north-east Tasmania

All 64 combinations of the three covariates resulted in fitted models within a delta AICc of 5.50 from the best model (lowest AIC) and with a maximum individual AICc weight of 0.05. In comparison, the AICc value of the NULL model was 11.95 higher than the lowest model. There was no support for the survey-specific detection probabilities in the model selection; the general detection probability with the camera traps was 0.18 (CI95%: 0.06 – 0.46) (Appendix S1).

Terrain ruggedness (TRI) was always negatively associated but the amplitude of the effect decreased with the larger buffer radius (Figure 2). The presence of low cover (heathland and scrub) was always positively associated, with a much stronger effect at the 1000 m buffer radius. Forest cover was positively associated at the 500 m buffer but was increasingly negatively associated at the larger buffer distances. Based on their relative AICc weights (Table 1), the abundance distribution of Tasmanian devils in our study was best explained by terrain ruggedness (TRI) at 500 m, the proportion of low cover within 1000 m and the proportion of forest cover within 500 m (Table 2).

Spatial prediction over the whole study area showed a heterogeneous distribution of the abundance in the landscape (Figure 3). The local abundance shown on the map reflects the number of devils expected to be detected if a sampling station was deployed in the 100m x 100 m cell for three times seven days (multiplied by the detection probability of 0.18). The highest local abundance (more than 5 individuals) was predicted in the coastal areas of the north, which comprise a mixture of heathland and forest and are predominately formal Protected Areas. Low altitude forests were preferred (local abundance of 2-5 individuals) to forests at higher altitude (local abundance of 1-2 individuals). Large open areas, mostly livestock pasture on farms, were the least populated with local abundance of less than 1 individual.

Table 1: N-Mixture abundance model average of the 64 candidate models with all combination of the three habitat covariates at a given buffer radius. TRI = average Riley's Terrain Ruggedness Index, Low cover = average presence or scrub and heathland, Forest cover = average presence of tree cover. pDet =probability of detection. The final radii were chosen as the highest AICc weight for each habitat covariate (^).

N-Mixture abundance model average					
	Estimate	**Std error**	**Z value**	**P value**	**AICc weight**
intercept	1.024	0.551	1.858	0.063	1
TRI					
500 m	-0.045	0.136	0.329	0.742	0.27 ^
1000 m	-0.045	0.140	0.320	0.749	0.26
3000 m	-0.037	0.140	0.262	0.793	0.24
5000 m	-0.029	0.130	0.224	0.823	0.23
Low cover					
500 m	0.053	0.187	0.283	0.777	0.12
1000 m	0.340	0.352	0.964	0.335	0.59 ^
3000 m	0.038	0.107	0.353	0.724	0.14
5000 m	0.033	0.093	0.357	0.721	0.15
Forest cover					
500 m	0.084	0.232	0.362	0.718	0.29 ^
1000 m	-0.025	0.166	0.153	0.879	0.22
3000 m	-0.035	0.127	0.276	0.782	0.22
5000 m	-0.057	0.147	0.388	0.698	0.27
pDet	-1.506	0.692	2.174	0.030	1

Figure 2: Average effect of the three habitat covariates on devil abundance: TRI (Terrain Ruggedness Index), low cover (heathland and scrubs) and forest cover at different buffer sizes (500 m, 1000 m, 3000 m, 5000 m). The error bars show the standard error for each estimate.

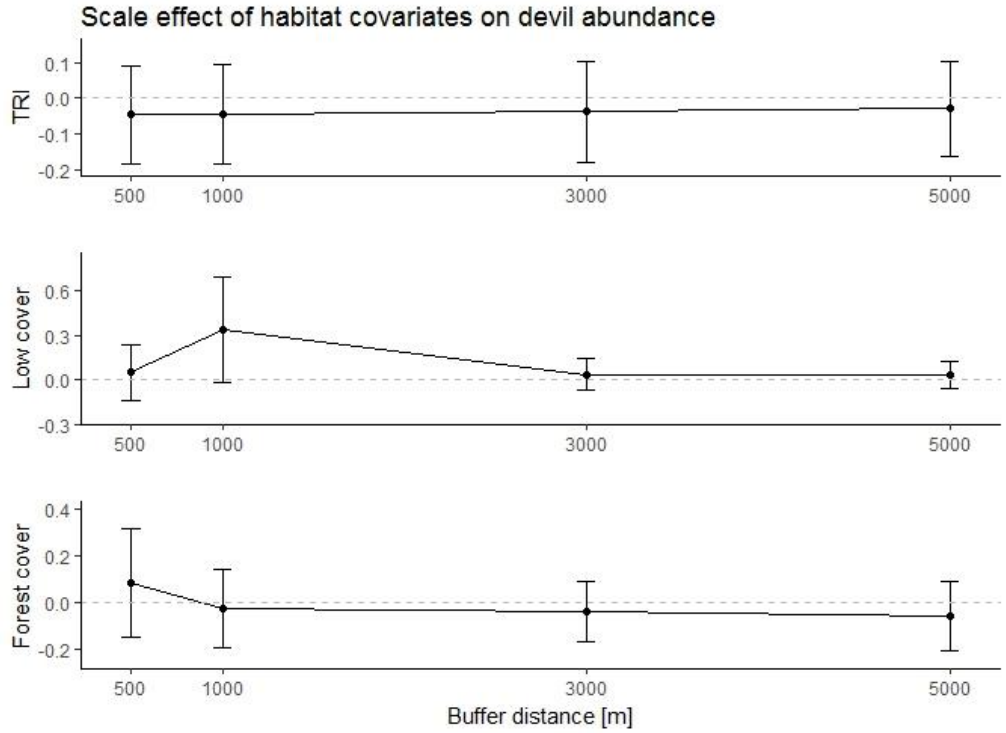


Table 2: N-mixture abundance model over the north-east Tasmania. TRI = average Riley's Terrain Ruggedness Index (500 m buffer), Low cover = average presence of scrub and heathland (1000 m buffer), Forest cover = average presence (500 m buffer). pDet=probability of detection. Significance levels are shown as: *p<0.05, **p<0.01, ***p<0.001.

	Estimate	Std error	Z value	P value
intercept	0.993	0.533	1.863	
TRI	-0.196	0.210	-0.932	0.351
Low cover	0.319	0.296	2.857	0.004**
Forest cover	0.758	0.265	1.078	0.281
pDet	-1.490	0.668	-2.23	0.026*

Figure 3: Spatial prediction of Tasmanian devil abundance over the North-East of Tasmania. Predicted map based on N-mixture model with three habitat covariates (TRI 500 m, low cover 1000 m and forest cover 500 m). The green dots represent the location of the 33 sampling stations with 2 camera traps set for 21 days. Low and high prediction represent the 95% confidence interval.

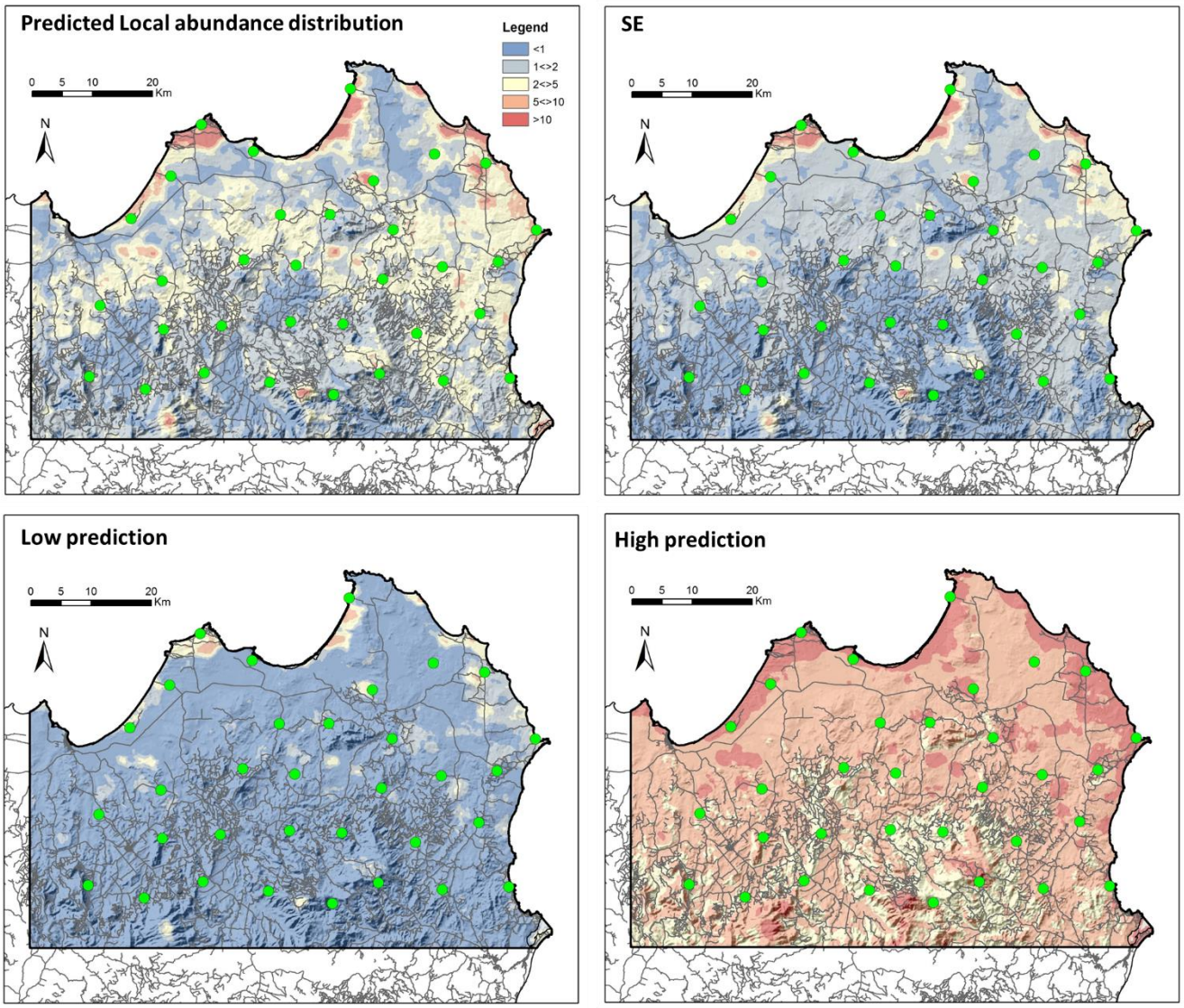


Table 3: Occupancy models for the three study areas (north-east: 33 camera traps for 21 days, Freycinet: 108 live traps for 7 days, wukalina: 40 live traps for 10 days). For each area, the presence/absence data was tested against the three habitat covariates from the final abundance model. TRI = average Riley's Terrain Ruggedness Index, Low cover = average presence or scrub and heathland, Forest cover = average presence of tree cover. pDet =probability of detection. Significance levels are shown as: *p<0.05, **p<0.01, ***p<0.001.

	Estimate	Std error	Z value	P value
North-East (2900 km²)				
intercept	0.960	0.607	1.582	
TRI 500	-0.311	0.713	-0.436	0.663
Low cover 1000	1.987	1.352	1.470	0.142
Forest cover 500	1.470	1.161	1.266	0.205
pDet	0.103	0.302	0.341	
Freycinet (300 km²)				
intercept	2.870	1.488	1.93	
TRI 500	1.805	0.895	2.02	0.044*
Low cover 1000	5.986	2.653	2.26	0.024*
Forest cover 500	0.734	0.615	1.19	0.233
pDet	-2.63	0.175	-15	
Wukalina (30 km²)				
intercept	-0.950	0.492	-1.882	
TRI 500	0.374	0.504	0.742	0.458
Low cover 1000	0.183	0.657	0.279	0.780
Forest cover 500	-0.156	0.588	-0.266	0.790
pDet	-1.85	0.378	-4.9	

2.3.2. Does abundance improve occupancy predictions?

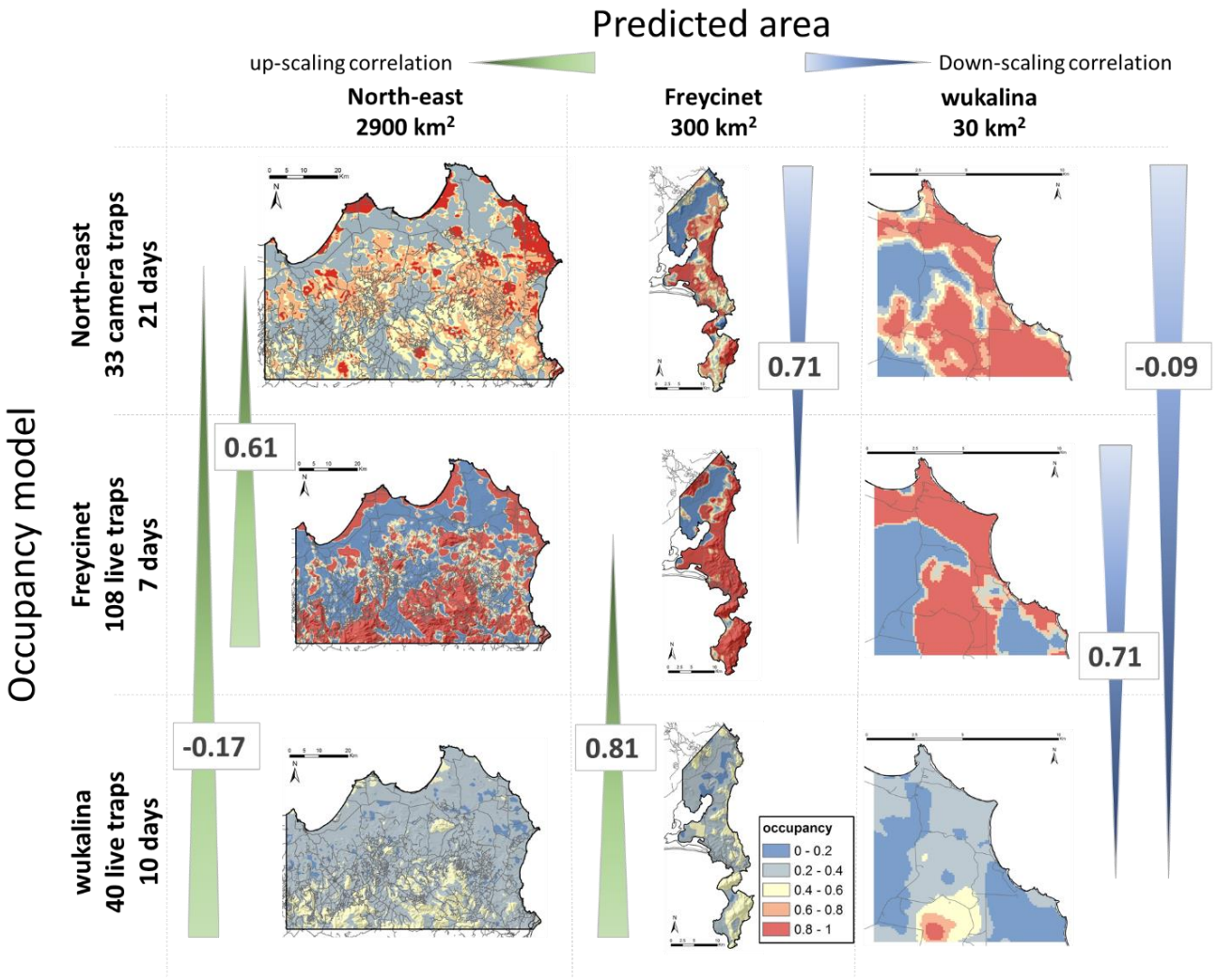
Occupancy distribution (Figure 4) was a good proxy for devil abundance distribution over the study area, with a correlation of rho = 0.88 (Spearman's rank test, S = 1.27 e+15). Within the presence/absence framework, the probability of detecting a devil at a sampling station was 0.52 (95%IC: 0.38 – 0.67). The effects of the three habitat covariates on occupancy were similar to the effects observed on abundance (Table 3). The predicted map of occupancy showed the strongest probabilities of occupancy on the coast (0.8 – 1.0). Forests at low altitudes (0.6 -0.8) were more suitable than forests in mountainous regions at higher altitudes (0.4 – 0.6). As with the results for modelling of abundance, the lowest occupancy was found in the open areas (0.2 – 0.4).

2.3.3. Up-scaling and down-scaling the occupancy predictions

In Freycinet, devils were strongly associated with low cover and terrain ruggedness, while forest cover presented a smaller but positive effect (Table 3). The predicted map showed a highly contrasted distribution, with high probabilities of occurrence across most of the peninsula and very low occupancy in the large open pastures of the north (Figure 4). In the smaller site of wukalina, occupancy was positively associated with terrain ruggedness and low cover and negatively associated with forest cover. The predicted map showed a higher occupancy around the slopes of Mt William and lowest occupancy in the large forest of the south-east and the large open pasture of the west.

Rescaling the prediction of the occupancy models over the three areas showed that the direction of the rescaling (up-scaling vs down-scaling) had no effect on the correlations but the amplitude of the rescaling (i.e. the degree of contrast between size of study area) made a difference. The prediction over the north-east (3000 km^2) and Freycinet (300 km^2) showed a good correlation with both up-scaling (Spearman's rank test *rho* = 0.61) and down-scaling (Spearman's rank test *rho* = 0.71). While medium and low altitudes showed similar occupancy (Figure 4), occurrence in the higher altitudes was consistently greater for the occupancy model based on the Freycinet trapping. The predictions over the two smaller areas showed a good correlation for both the up-scaling (Spearman's rank test *rho* = 0.81) and the down-scaling (Spearman's rank test *rho* = 0.71). The comparison from the large-scale (North-East) occupancy model with the small-scale model (wukalina) showed a very poor correlation (Spearman's rank test *rho* = -0.17 for upscaling and *rho* = -0.09 for downscaling).

Figure 4: Rescaling of the predicted occupancy probabilities over the three study areas. Each row represents one occupancy model and each column represents the area over which the model is predicted. Spearman's rank test correlations (rho) are given for the upscaling and downscaling of the areas compared to the empirical predicted map.



2.4. Discussion

Key results of our analysis are that: 1) the spatial scale of the area in which the habitat covariates are calculated (size of the buffer) has a strong effect on predictions of abundance for Tasmanian devils; 2) occupancy predictions are strongly correlated with abundance predictions for devils, but abundance carry finer information within the most favourable habitats; and 3) changing the spatial scale of the empirical survey has a strong effect on occupancy prediction but the direction of the rescaling (up-scaling or down-scaling) does not affect the outcome. This study demonstrates that when possible, modelling the distribution of abundance should be favoured over modelling occupancy to provide more accurate distribution maps. Integrating a multiscale framework will also enhance the accuracy of the prediction which could then be used as support for conservation strategies.

Spatial scale has an important influence in how different types of landscape features are perceived by individual organisms as they make behavioural decisions on where to move, and so influences their abundance distribution. Different types of landscape features show different patterns of relative influence across scales (Martínez-Miranzo et al., 2016), reflecting the significance of these habitat elements for different scales of movement activity. Proximal or immediate movement (500m radius scale for devils) reflects energetic constraints as individuals respond to the physiological effort of moving through the terrain and resource availability. The best model prediction of devil abundance included a negative association with terrain ruggedness and a positive association with forest cover at the scale of 500m radius around the camera traps. Avoiding rugged terrain is an obvious behavioural response to conserve energy. The positive association with forest cover in the 500 m radius reflects the use of forest/open grassland ecotone, as demonstrated in detailed movement studies in healthy populations (Jones and Barmuta, 2000; Andersen et al., 2017b). Devils hunt the edges between forest and open grassland, where they can intercept their primary herbivore prey, macropods and possums (Andersen et al., 2017a), that take refuge in the forest during the day and emerge into the open to feed on grass at night. At a slightly larger scale relevant to nightly foraging (1000m radius), devils are attracted to a high proportion of low cover. The extent of low cover is mostly driven by low altitude, flat, coastal heathland, which is patchily distributed with no patches larger than a couple of square kilometres and thus presenting a large amount of edges. These areas abound in marsupial herbivores unless they are extensively cleared for livestock grazing, areas which our analyses indicate are strongly

avoided by devils. At the scale of the home range (3000m radius), devils are negatively associated with forest cover, rugged terrain and higher altitudes, which co-occur at high extent in the more mountainous parts of the study area and are also associated with higher rainfall and dense wet forests that support lower prey densities (Rounsevell et al., 1991).

When possible, modelling the local abundance of a species provides a more accurate tool to establish and monitor changes to its distribution than does occupancy. The abundance-occupancy relationship is a central ecological process driving population dynamics and, for most animal taxa, this relationship is positive (Zuckerberg et al., 2009; Roney et al., 2015). Based on our results, the Tasmanian devil is no exception, but local mismatches were still present, especially in areas of high occupancy, a pattern previously described by Sileshi et al. (2009). If occupancy and abundance are mostly correlated for large-scale socio-demographic traits, local history of occurrence and competition likely influence abundance at smaller scale (Nielsen et al., 2005). Monitoring abundance provides more accurate information for conservation (Méndez et al., 2018), but it also comes with higher data requirements that cannot always be met with available resources. The generally strong correlation between abundance and occupancy models support the latter as a valuable alternative for monitoring the distribution of populations for conservation (Gormley et al., 2015).

Our study shows that occupancy predictions are directly influenced by the spatial scale and methods of the survey, supporting the growing need for multiscale frameworks in species distribution modelling. The three data sets used to test rescaling of occupancy predictions differed in both the survey method and the area of the study site. When using point sampling, the density of detectors (camera traps or live traps in our study) has a marginal effect on the predicted occupancy (Steenweg et al., 2018), which leaves the duration of the survey and the spatial scale as potentially confounding factors. For mobile species, a longer survey period can increase the probability of detecting an individual within its home range, an effect supported by our results and directly accounted for with the occupancy model (MacKenzie et al., 2002). Scale effects in landscape ecology are widely recognized (Schneider, 2001), and the influence of scale on occupancy is starting to be acknowledged (McDonald et al., 2015; Steenweg et al., 2018). In our study, reducing the spatial scale of the survey resulted in more homogenous landscapes, that contained a subset of the wider range of biotic and abiotic features present in the region. Local contrasts thus masked the larger scale patterns of distribution. The lower correlations between the largest and the smallest areas and

the absence of directional difference (up-scaling vs down-scaling) suggest that the scale effect on occupancy is a continuous process. Integrating the influence of the landscape on species distribution at different scales could then provide a unique support to design efficient conservation strategies, both locally and regionally (Pitman et al., 2017; Zwolicki et al., 2018).

2.5. Implications for conservation

How does the more detailed information from the multiscale abundance-based distribution modelling assist with conserving the Tasmanian devil, a wide-ranging carnivore that is endangered by a recently emerged infectious disease (EID)? The more explicit abundance models show that, in the long-diseased areas of the north-east, devils are only present in reasonable numbers in coastal complexes and to a lesser degree in low altitude forests; mountains and large open areas of livestock pasture have few devils. With an initially rapid and then sustained reduction of 90% of the population following DFTD outbreak 20 years ago, devils are now virtually restricted to their core preferred habitat but with a few individuals remaining in suboptimal areas, creating a meta-population network. Extreme devil mortality from this single-host disease means that surviving host populations have much reduced competition for greater *per capita* resources. At a local scale, increased *per capita* resources has led to a reduction of female home range size and a clustered spatial organisation (Chapter 3 of the thesis). At a larger scale, female dispersal distances have reduced, reflecting the common pattern in female mammals for resources to drive behavioural decisions in natal dispersal (Lachish et al., 2011). Natal dispersal (Hanski and Simberloff, 1997) and habitat connectivity (Fattebert et al., 2015) are the main structural mechanisms underlying meta-populations dynamics. Both the high loss of abundance and its heterogenous distribution observed in north-eastern Tasmania suggest the establishment of a meta-population demography for devils in long-diseased areas.

The change from large, well-connected and genetically homogenous populations prior to DFTD outbreak (Jones et al., 2004; Miller et al., 2011; Hendricks et al., 2017) to a meta-population structure in spatial organisation could be key factors for the long-term resilience of devil populations and the transition of DFTD from epidemic to endemicity. The devil and its transmissible cancer can be considered as a host-pathogen system with a high mortality

rate and a strongly frequency-dependent transmission (McCallum et al., 2009). While the large homogeneous populations at the beginning of the epidemic favoured a rapid spread of the disease with a strong impact on host densities, the emerging structure of a meta-population in the long diseased areas provides ground for host resilience (Sah et al., 2017; Siska et al., 2018). The high modular structure of a meta-population is known to slow the spread of a pathogen by trapping it within small densely interconnected clusters of individuals (Cross et al., 2005). Then, the dynamic mosaic of local extinction and recolonization with healthy individuals can desynchronize the epidemics and the dispersal of the hosts, improving the long-term survival of the whole meta-population (Fox et al., 2017). Additional large-scale surveys of devil abundance could provide the perfect dataset to empirically test this theory. Meta-population dynamics, combined with rapid evolution of host resistance (Margres et al., 2018a; Margres et al., 2018b) and tolerance (Ruiz-Aravena et al., 2018b) to DFTD based on standing genetic variation (Epstein et al., 2016) and long-period oscillations of host and disease indicated by individual-based models incorporating pathogen load and transmissibility (Wells et al., 2018), point towards long-term persistence of Tasmanian devils and disease endemicity. In this scenario, close monitoring of the wild populations should be preferred to active intervention.

2.6. Conclusion

Our study shows that the accuracy of species distribution models, widely used for conservation management, can be greatly improved by modelling the abundance of the species of interest over using only presence/absence records. The availability of occurrence information at different spatial scale in our study system highlighted the need to develop accessible multiscale frameworks to better inform management policies of endangered species. In the context of DFTD epidemics, we demonstrate the need for additional large-scale surveys with temporal replicates of the long-diseased populations to predict the long-term resilience of the host. Recent integrative studies showed the high potential of these multiscale approach for both conservation (Fattebert et al., 2018) and epidemiology (McDonald et al., 2017).

2.7.References

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2.8. Appendix S1

Table S1: Model selection (based on AICc value) of the 64 combination for the three habitat covariates with increasing buffer sizes.

		Terrain Ruggedness Index				Low cover				Forest cover								
pdet	**Int**	**500**	**1000**	**3000**	**5000**	**500**	**1000**	**3000**	**5000**	**500**	**1000**	**3000**	**5000**	**df**	**logLik**	**AICc**	**delta**	**weight**
-1.48	0.98		-0.21				0.76			0.33				5	-92.34	196.90	0.00	0.05
-1.49	0.99	-0.20					0.76			0.32				5	-92.36	196.94	0.04	0.05
-1.50	1.00			-0.22			0.75			0.34				5	-92.39	196.99	0.09	0.05
-1.49	0.99				-0.20		0.75			0.34				5	-92.45	197.13	0.23	0.05
-1.59	1.08	-0.10					0.42						-0.16	5	-92.68	197.59	0.69	0.04
-1.57	1.07		-0.10				0.42						-0.15	5	-92.70	197.61	0.71	0.04
-1.56	1.06			-0.06			0.43						-0.16	5	-92.78	197.78	0.88	0.04
-1.55	1.05				-0.04		0.44						-0.16	5	-92.80	197.83	0.92	0.03
-1.57	1.07	-0.11					0.45					-0.10		5	-92.87	197.97	1.06	0.03
-1.56	1.06		-0.11				0.46					-0.10		5	-92.88	197.98	1.08	0.03
-1.50	1.02	-0.15					0.56				0.06			5	-92.96	198.14	1.23	0.03
-1.49	1.01		-0.15				0.56				0.06			5	-92.96	198.14	1.24	0.03
-1.55	1.06			-0.08			0.46					-0.10		5	-92.96	198.15	1.24	0.03
-1.54	1.05				-0.07		0.46					-0.10		5	-92.99	198.20	1.29	0.03
-1.51	1.02			-0.14			0.55				0.05			5	-93.04	198.30	1.39	0.03
-1.49	1.01				-0.12		0.55				0.04			5	-93.08	198.38	1.47	0.03
-1.56	1.08	-0.19						0.25					-0.28	5	-93.72	199.66	2.75	0.01
-1.54	1.06		-0.19					0.25					-0.28	5	-93.75	199.73	2.82	0.01
-1.57	1.08	-0.12							0.24		-0.33			5	-93.76	199.74	2.84	0.01
-1.56	1.07		-0.12						0.24		-0.33			5	-93.78	199.78	2.87	0.01
-1.55	1.06	-0.20							0.22				-0.30	5	-93.81	199.85	2.94	0.01

		Terrain Ruggedness Index				Low cover				Forest cover								
pdet	**Int**	**500**	**1000**	**3000**	**5000**	**500**	**1000**	**3000**	**5000**	**500**	**1000**	**3000**	**5000**	**df**	**logLik**	**AICc**	**delta**	**weight**
-1.53	1.05		-0.20						0.22				-0.30	5	-93.85	199.92	3.02	0.01
-1.55	1.07			-0.07					0.23		-0.35			5	-93.86	199.94	3.04	0.01
-1.54	1.06				-0.05				0.23		-0.36			5	-93.88	199.98	3.08	0.01
-1.53	1.06			-0.15				0.24					-0.28	5	-93.93	200.09	3.19	0.01
-1.32	0.88	-0.35				0.76				0.47				5	-93.94	200.10	3.20	0.01
-1.54	1.06	-0.14						0.26			-0.28			5	-93.98	200.18	3.27	0.01
-1.35	0.91			-0.38		0.74				0.50				5	-93.98	200.18	3.28	0.01
-1.53	1.05		-0.14					0.26			-0.28			5	-93.99	200.21	3.31	0.01
-1.51	1.04				-0.12			0.24					-0.30	5	-94.00	200.23	3.32	0.01
-1.29	0.87		-0.35			0.75				0.46				5	-94.00	200.23	3.32	0.01
-1.57	1.09	-0.19						0.27				-0.24		5	-94.01	200.24	3.34	0.01
-1.55	1.07		-0.19					0.27				-0.25		5	-94.05	200.31	3.41	0.01
-1.57	1.08	-0.20							0.24			-0.27		5	-94.06	200.34	3.44	0.01
-1.53	1.06			-0.11				0.24			-0.29			5	-94.06	200.35	3.45	0.01
-1.51	1.04			-0.15					0.21				-0.31	5	-94.07	200.37	3.46	0.01
-1.52	1.05				-0.10			0.24			-0.30			5	-94.09	200.40	3.50	0.01
-1.55	1.07		-0.19						0.24			-0.28		5	-94.10	200.41	3.51	0.01
-1.48	1.02				-0.12				0.21				-0.33	5	-94.15	200.53	3.62	0.01
-1.32	0.89				-0.34	0.71				0.45				5	-94.17	200.57	3.66	0.01
-1.55	1.08			-0.16				0.26				-0.25		5	-94.20	200.62	3.71	0.01
-1.41	0.97	-0.17				0.27							-0.22	5	-94.22	200.65	3.75	0.01
-1.40	0.96		-0.17			0.27							-0.22	5	-94.24	200.70	3.79	0.01
-1.53	1.06				-0.14			0.26				-0.26		5	-94.25	200.72	3.82	0.01
-1.54	1.07			-0.16					0.22			-0.29		5	-94.28	200.79	3.89	0.01
-1.52	1.05				-0.13				0.22			-0.30		5	-94.35	200.92	4.01	0.01
-1.40	0.97			-0.14		0.27							-0.21	5	-94.35	200.92	4.02	0.01
-1.39	0.95				-0.12	0.27							-0.22	5	-94.41	201.04	4.14	0.01
-1.40	0.97	-0.18				0.30						-0.16		5	-94.44	201.11	4.21	0.01

		Terrain Ruggedness Index				Low cover				Forest cover								
pdet	**Int**	**500**	**1000**	**3000**	**5000**	**500**	**1000**	**3000**	**5000**	**500**	**1000**	**3000**	**5000**	**df**	**logLik**	**AICc**	**delta**	**weight**
-1.39	0.95		-0.18			0.30						-0.16		5	-94.47	201.16	4.25	0.01
-1.40	0.97			-0.17		0.30						-0.15		5	-94.56	201.34	4.43	0.01
-1.35	0.93	-0.18				0.33					-0.11			5	-94.59	201.41	4.50	0.01
-1.34	0.92		-0.18			0.32					-0.12			5	-94.61	201.44	4.54	0.01
-1.38	0.96				-0.14	0.30						-0.16		5	-94.61	201.45	4.54	0.01
-1.37	0.94			-0.17		0.30					-0.13			5	-94.66	201.54	4.63	0.01
-1.46	1.02	-0.25						0.33		-0.09				5	-94.70	201.62	4.71	0.01
-1.35	0.94				-0.15	0.29					-0.15			5	-94.70	201.63	4.73	0.01
-1.44	1.00		-0.25					0.33		-0.09				5	-94.74	201.70	4.80	0.00
-1.46	1.01	-0.24							0.28	-0.17				5	-94.76	201.74	4.83	0.00
-1.44	1.00		-0.24						0.27	-0.17				5	-94.80	201.82	4.92	0.00
-1.46	1.02			-0.25				0.30		-0.09				5	-94.84	201.91	5.00	0.00
-1.44	1.00				-0.23			0.30		-0.10				5	-94.92	202.06	5.15	0.00
-1.44	1.01			-0.21					0.25	-0.18				5	-94.96	202.14	5.24	0.00
-1.42	0.99				-0.18				0.25	-0.19				5	-95.04	202.30	5.39	0.00
-0.69	0.61													2	-102.23	208.86	11.95	0.00

CHAPTER 3. Changes in spatial organization following an acute epizootic: Tasmanian devils and their transmissible cancer.

"Not all those who wander are lost"

J.R.R. Tolkien

3.1. Introduction

Acute disease outbreaks may decrease the density of their hosts, and in so doing can alter the spatial and social structure of the host population. Classic epidemiological models focus on temporal changes in host density to predict disease transmission (De Castro and Bolker, 2005; Cooch et al., 2012). A pathogen with a density-dependent transmission can die out when the host population drops below the threshold required to maintain the epidemic (Deredec and Courchamp, 2003). Pathogens with frequency-dependent transmission, on the other hand, lack this threshold and can, in theory, drive the host population to extinction (McCallum, 2012). Yet, if mortality is high, population decline can be rapid with consequent changes in per-capita resource availability. If resources are well distributed in the landscape, inter-individual competition should lead to higher spatial segregation (Kjellander et al., 2004). But if resource distribution is heterogeneous, remnant individuals will most likely concentrate their activity within the areas of higher resources, resulting in a patchy distribution of the hosts (Newsome et al., 2013). These often-neglected ecological feedbacks are non-trivial and may influence ongoing disease transmission dynamics.

Tasmanian devil facial tumour disease (DFTD) is a host-specific transmissible cancer with an almost 100% mortality rate that has resulted in sustained local population declines of up to 95% (McCallum et al., 2007). Transmission is via injurious biting and direct transfer of live tumour cells, particularly associated with contacts during mating season behaviours (Hamede et al., 2008). The link between transmission and the annual mating season means that DFTD has a strong component of frequency-dependent transmission. Yet, more than twenty years after the DFTD outbreak, no local extinction of the host has been reported. Devils are still present, albeit at very low densities, even in long diseased areas (Lazenby et al., 2018). While studies have focussed on the epidemiology (Pye et al., 2016; Wells et al., 2017) and rapid evolutionary response of devils (Epstein et al., 2016; Wright et al., 2017), no study has reported on the effect of the disease on the spatial organisation of the host populations.

The structure of the spatial organisation of a species is classically defined by the size and overlap of individual home ranges (Arden-Clarke, 1986; Belcher and Darrant, 2004; Fattebert et al., 2016). While most ecologists agree on the classical concept of home range given by Burt (1943), there is no universally accepted method to quantify and represent home range (Worton, 1987; Walter et al., 2015). For decades, home ranges have been calculated using individual movements recorded by telemetry (Harris et al., 1990; Cagnacci et al., 2010), a rapidly evolving field due to advances in technology. While providing unprecedented knowledge of animal behaviour, the most recent estimators of home range rely on high resolution tracking data that is often not available with historical data. In addition, as reviewed by Hebblewhite and Haydon (2010), although very high frequency (VHF) radiotracking usually provides a lower frequency of location fixes with a lower precision than those derived using global positioning system (GPS), its much lower cost makes it a valuable choice still for wildlife ecologists (Jerosch et al., 2017).

While the technology differs, VHF and GPS tracking data do provide comparable estimations of home range size, given similar sampling effort (Pellerin et al., 2008). This has been demonstrated in studies of either the same individuals (white-tailed deer, (Fieberg and Kochanny, 2005)) or simultaneously on different individuals in the same population (wild turkeys, (Niedzielski and Bowman, 2016) and American alligator, (Skupien et al., 2016)). While these studies relied on long-term low frequency VHF tracking to complement the fine-scale GPS data, a challenge for conservation biologists is to compare data from recent GPS tracking with data collected during past VHF studies, before GPS tracking collars became available. In this study, we use location data of devils collected in the same area before (VHF) and fifteen years after (GPS) the outbreak of DFTD. After accounting for sampling heterogeneity (frequency, number of locations and tracking duration) between the technologies, we assess the impact of the decline in population density on the size and overlap of the home ranges and discuss the potential implication of our results for disease transmission.

3.2.Materials and methods

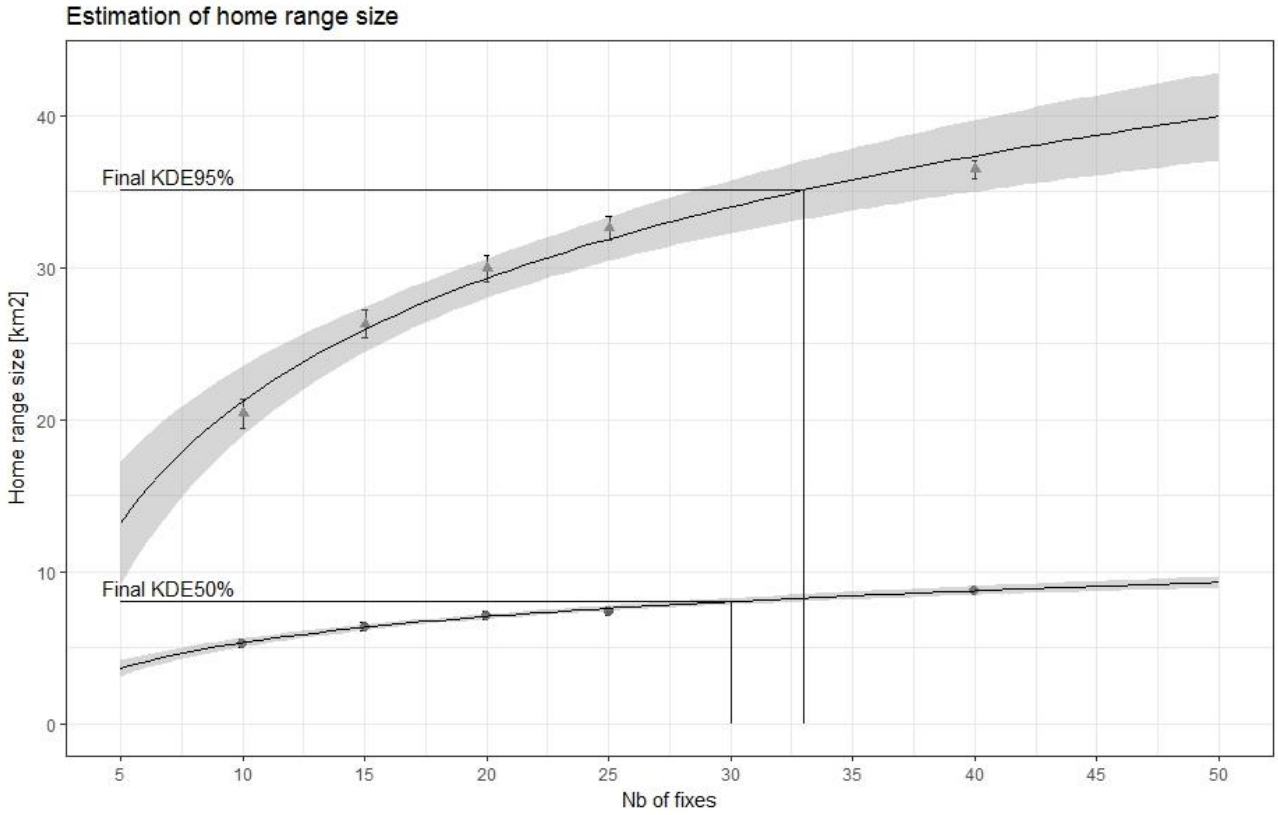
The study took place on the Freycinet Peninsula (42°03’53’’S, 148°17’14’’E), a topographically varied and rugged landscape on the East Coast of Tasmania, Australia (Lachish et al., 2007). The 100 km^2 area is part of a long-term study aimed at monitoring the devil population and DFTD epidemic dynamics (Jones et al., In review). During the Austral winter (June-July), the study area has been monitored with 60 cage traps (2001), 43 PVC pipes traps (2015) and 49 PVC pipe traps (2016) set over seven contiguous nights. Individual identification of the animals (ear tattoos <2004; microchips >2003) allowed us to use a spatially-explicit capture-recapture (SECR) model (Efford et al., 2009) to estimate the winter population densities by sex (female vs male) and age (adults vs subadults). The SECR models were fitted with a hazard half normal detection function and the Nelder and Mead (1965) maximization method of the likelihood. We followed Efford et al. (2016) by replacing σ (the spatial scale parameter of the SECR models) in the detection function by a density (D) dependent parameter $k = \sigma \sqrt{D}$ allowing us to calculate an index of home range overlap $S_{95}=6\sigma k^2$. Density analyses were performed in R (2017, version 3.3.3) with the package “secr” v3.1.0.

During May 2001, before the DFTD outbreak, 42 VHF transmitters were fitted to male and female Tasmanian devils. Four daily radiolocations were attempted for each collar using four fixed towers and a mobile antenna mounted on a vehicle. Locations of the animals were calculated by triangulation using R (2017, version 3.3.3) with the package “sigloc” v0.0.4 (Lenth, 1981). Only animals with at least 15 location fixes were considered for this study (n=19; 7 females and 12 males). In 2015 and 2016, respectively, 14 and 15 years after the disease outbreak, GPS collars were deployed in the same study area between August and December. Tracking data was available for 5 individuals in 2015 (3 females and 2 males) and 7 in 2016 (5 females and 2 males). Two females were fitted with a GPS collar in both 2015 and 2016. GPS location attempts were set hourly over each night between 17:00 and 7:00. As none of the animals tracked for this study presented with clinical signs of DFTD, we were able to assess the impacts of the disease-driven population decline on individual home ranges, rather than the direct pathological impacts of the disease.

Following Pellerin et al. (2008), VHF and GPS tracking records can provide comparable estimations of home range sizes, using the kernel density estimator (KDE) and a fixed smoothing parameter, when the sampling effort is similar. In our study, we used a constant smoothing parameter (h) of 500 m, representing an averaged "href" value using bivariate normal KDE on individual tracking data (Worton, 1989). As the duration of the VHF tracking was shorter than the GPS tracking, we divided the GPS data into consecutive 30-days periods. The frequency of fixes was also lower and less regular for the VHF tracking (average of 26 locations, range: 16-43) than for the GPS tracking (average of 229 locations, range: 130-303). To accommodate for this heterogeneity in sampling effort, we first estimated an average (based on one hundred replicates) home range size (95% KDE) and core area (50% KDE) for an increasing fractions of location fixes randomly selected from the tracking data (sequentially 10, 15, 20, 25, 40, stopping at the total available for each individual). We then fitted a logarithmic regression (Haines et al., 2009) on the sequential individual areas (including the maximum area estimated with the whole data set for individuals with less than 40 locations) and, following Odum and Kuenzler (1955), we considered the final home range sizes (95% and 50% KDE) as the first interval after which any additional location fix resulted in less than one percent increase of the predicted area (Figure 1).

To spatially represent the final home ranges (95% KDE), we first drew one hundred home ranges based on the repeated random selection of ten location fixes. Using a 50m x 50m grid over the whole study area, we calculated the number of times each individual cell was included in the home ranges. The final shape of the home range was obtained by joining the cells according to their ranking, until the area of the shape matched the final areas previously calculated on the logistic regressions. The analysis of home-range overlap was robust only for female devils, because of the low number of males tracked in 2015 and 2016. We measured the proportion of the home range overlap for each possible pair of females (A and B, with the assumption that $A \cap B \neq B \cap A$) with consideration that age (2 years old vs 3+ years old) may influence social spacing. We used a Student's t-test to compare the home range sizes (95% KDE and 50% KDE) and the proportion of overlap between individuals before (2001) and after (2015-2016) the DFTD outbreak. All analyses were performed in R (2017, version 3.3.3) using the packages "adehabitatHR" and "rgeos".

Figure 1: Estimation of the final home range size (95% kernel density estimator, KDE) and core area (50% KDE) for one female devil (TD.625) tracked with a GPS collar in 2016. Each triangle (95%KDE) and circle (50%KDE) represent the average size (y-axis) and 95% confidence interval of the home range based on 100 replicates of randomly selected location fixes from the tracking data (x-axis). The curves represent the logistic regressions fitted on the average sizes and the grey area the 95% confidence interval of the predicted regression. The final value for the home range and core area sizes correspond to the first interval of location fixes with an area increase of less than 1%.



3.3.Results

Prior to the disease outbreak, the population structure of devils in the study area was balanced between males and females with more adults (2+ years) than subadults (independent 1 year old) (Table 1). In 2015, after the outbreak of DFTD, the density of adults decreased by 4 and 7 times for males and females, respectively. The density of subadults in the population remained unaltered. In 2016, the adult densities remained lower than in 2001 but the female population increased slightly compared to 2015. This overall decline in adult density following the DFTD epidemic was accompanied by a reduction of the home range overlap index S_{95} (Table 1), although the confidence intervals still overlapped.

Table 1: Population densities of Tasmanian devils on the Freycinet Peninsula before the DFTD epidemic (2001) and 15 years after disease emergence (2015 and 2016).

Year	Sex	Adults [n/km^2]	Subadults [n/km^2]	λ0	k	S_{95}
2001	males	0.169 (0.106-0.271)	0.085 (0.044-0.164)	0.051 (0.038-0.070)	0.713 (0.542-0.938)	9.596 (5.546-16.601)
2001	females	0.198 (0.135-0.289)	0.150 (0.092-0.247)			
2015	males	0.043 (0.018-0.106)	0.087 (0.046-0.165)	0.048 (0.028-0.082)	0.355 (0.217-0.581)	2.381 (0.890-6.371)
2015	females	0.026 (0.011-0.064)	0.061 (0.029-0.130)			
2016	males	0.055 (0.022-0.135)	0.066 (0.029-0.151)	0.027 (0.020-0.038)	0.522 (0.409-0.666)	5.137 (3.158-8.357)
2016	females	0.066 (0.049-0.089)	0.066 (0.029-0.151)			

Densities estimated using spatially explicit capture recapture models (SECR). λ0 = cumulative hazard of detection; k = density dependent scale factor; and S_{95} = index of overlap in home range. Densities were modelled as sex (male *vs* female), age (adult *vs* subadult) and year (2001, 2015 and 2016) specific, λ0, k and S95 were dependent on year only. 95% confidence intervals for all values are indicated in brackets.

Following the decrease in population density, female home ranges were significantly smaller (95% home range: t = 2.599, df = 12.096, p = 0.023) (Figure 2), with a similar trend for the core areas (50% home range: t = -1.774, df = 10.618, p = 0.105). We found no apparent change in male home ranges and core areas (95% home range: t = 1.108, df = 13.901, p = 0.287 and 50% home range: t = -0.958, df = 12.49, p = 0.356 respectively).

As devil density declined, female home range overlap reduced from 40% in 2001 to 18% in 2015-2016 (t = -3.165, df = 44.779, p = 0.003), confirming the decrease of the S_{95} estimates from the SECR modelling. This decrease was stronger between females of the same age (3+ years old: from 63% to 17%; 2 years old: from 27% to 4%) than between older and younger females (2 years old ∩ 3+ years old: from 40% to 26%). As shown in Figure 3, this resulted in 2016 in two spatially segregated pairs of females, TD.522 & TD.979 (red home ranges) in the west and TD.823 & TD.455 (blue home ranges) in the centre. Both pairs included one older female (3+ years old) and one younger female (2 years old). The home range of the last female (TD.635, purple home range) was further south-east but still overlapped slightly with the central pair.

Figure 2: Distribution of home range (95% KDE) and core area (50% KDE) sizes for female and male devils before the DFTD outbreak (2001, green) and 15 years after DFTD arrival (2015-2016, orange).

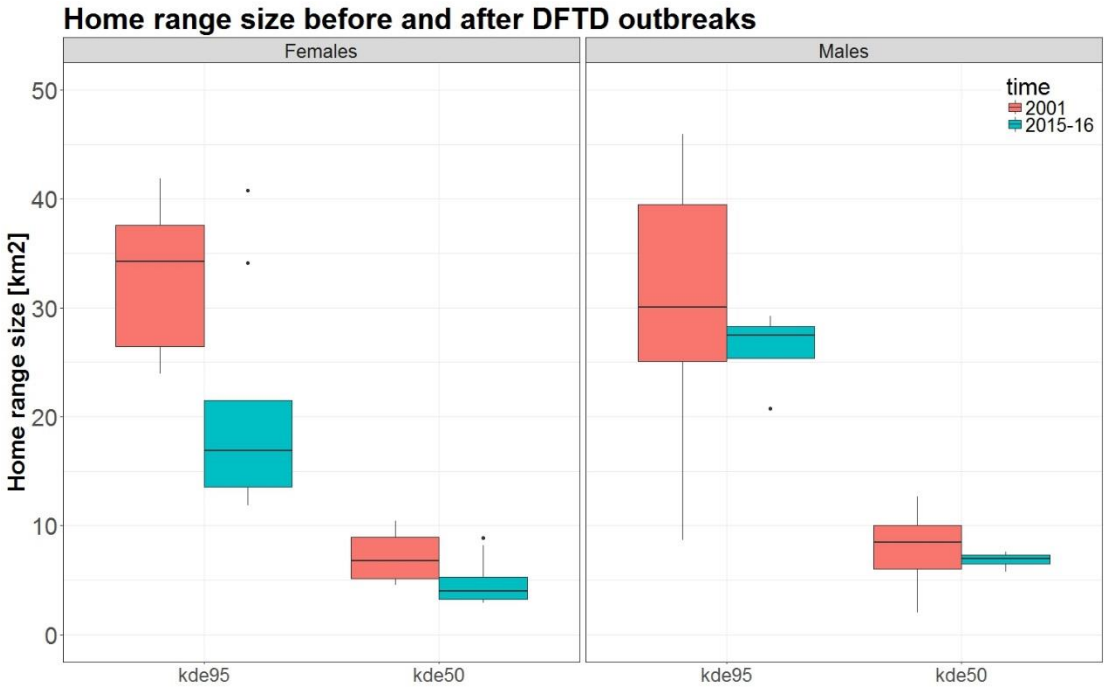
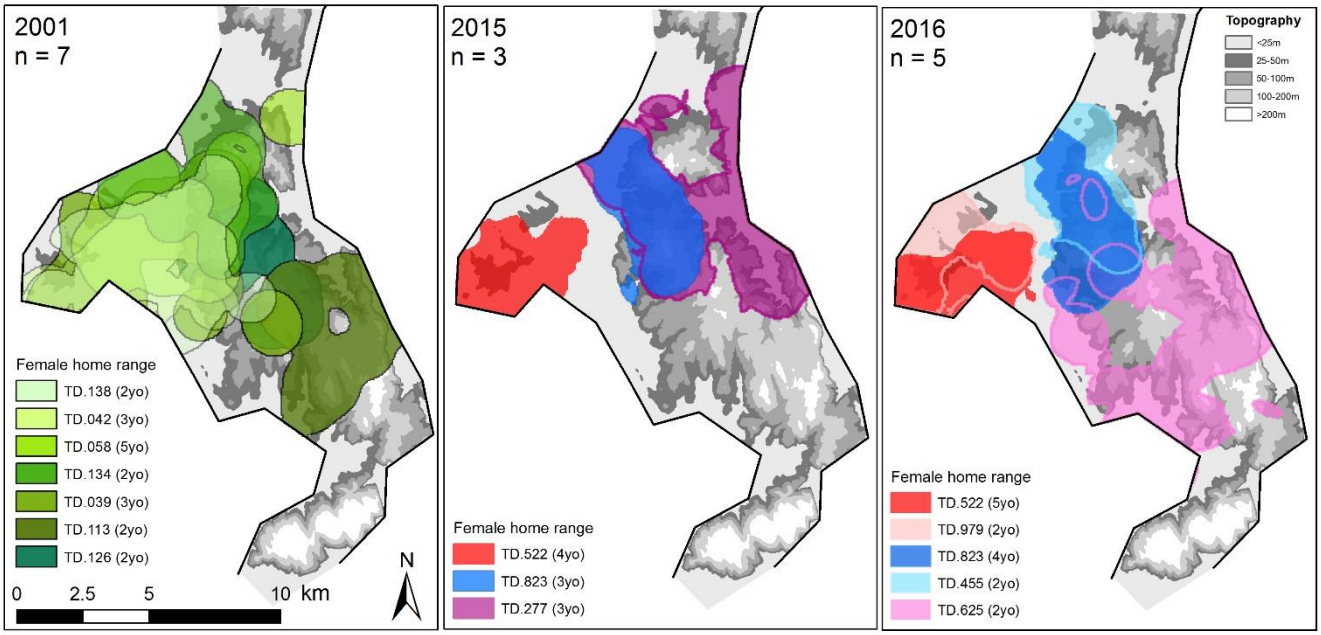


Figure 3: Spatial representation of female home ranges (95% KDE) before DFTD outbreak (2001) and 15 years after DFTD arrival (2015 and 2016). Two females (TD.522 and TD.823) were tracked both in 2015 and 2016. The black lines represent the coast and the grey scaled background shows the topography.



3.4.Discussion

Our results show that the DFTD epidemic resulted in a strong decline in population density, particularly for adult devils; and more for female than male devils. Density decline was accompanied by a response in spatial organisation, resulting in reduced home range size as well as lower overlap between same sexes and ages. Our study highlights the value of utilizing past datasets to understand current demographic and epidemiological patterns.

The downside of using pre-existing data is that we cannot go back in time to modify or add data. The data set on home ranges from 2001 is the only pre-DFTD tracking data available for devils from a site where we also have tracking data collected after DFTD-caused population decline, albeit necessitating the comparison of VHF and GPS data. We will be able to spatially replicate our study once DFTD reaches the northwest coast of Tasmania and causes devil population decline. Then, we will be able to more finely compare changes in ranging behaviour, using GPS tracking data that was collected in 2012 and 2013 (Andersen et al., 2017b) in one of the last healthy populations in Tasmania.

Our results are supportive of sex-biased differences in spatial organisation mediated by resource availability. The decrease in devil density owing to DFTD likely resulted in an increase of resources per capita. The observed changes in female home range size are therefore in accordance with the general theory that spatial ecology of female mammals is driven by food resources and energetic requirements (Lawson Handley and Perrin, 2007; Saïd et al., 2009). With an increase in per-capita resources, females can reduce the energy and the time necessary to cover their own needs and to provision for their young, which generally result in smaller home range sizes (Sandell, 1989; Maletzke et al., 2014). In contrast, the spatial organisation of males in solitary carnivores species is driven by the opportunities for paternity success, which include the needs to maintain dominance (Clapham et al., 2012) and assess female reproductive status (Ramsey et al., 2002), two mechanisms reflected in our study by the higher stability in male home range sizes.

Although devils do not show exclusive territorial behaviour, when the opportunity arises through an infectious disease reducing density in relation to local resources leading to smaller home range size, females are likely to spread out to reduce inter-individual competition. Most scavenging carnivores, devils in particular (Pemberton and Renouf, 1993), display individual scrounging behaviour (i.e. exploiting resources discovered by others) leading to communal feeding. While scrounging individuals may allow for higher predator densities for the same amount of resources (Coolen et al., 2007), their proportion in the population should decrease when the resources become more abundant (Beauchamp, 2008). In low densities with high resources, an individual is more likely to find its own food than it is to benefit from conspecific foraging and the cost of interindividual interactions become too high. With the increase in per-capita resources following DFTD outbreak, conspecific tolerance among devils should then decrease and females are likely to show a higher spatial segregation (Gehrt and Fritzell, 1998). This may explain the stronger reduction of home range overlap observed between females of the same age, but not the aggregated spatial structure observed in 2016.

As with home range size, female dispersal is driven by the availability of food resources to provision young (Gehrt and Fritzell, 1998) whereas male dispersal is driven by in-breeding avoidance (Lawson Handley and Perrin, 2007). The decline in population density following the DFTD outbreak resulted in a reduction in dispersal distance in female devils but not in males (Lachish et al., 2011). This reduced dispersal should lead to an increase in the numerical size of clusters of related females from multiple generations (Støen et al., 2005; Fattebert et al., 2016; Holmala et al., 2018). Although nuanced by the low survival rate in long DFTD infected populations, matrilineal clusters may still arise in devil populations with one or more daughters staying close to the maternal home range. This may explain the heterogeneous distribution of female home ranges observed in 2016. The age structure of the high overlapping pairs may indeed indicate kin relationship, but further genetic analyses, using tissue samples taken during the trapping, are necessary to confirm this relatedness.

The observed density-related changes in spatial organisation would alter the network of social contact patterns between individuals in the population with consequences for disease transmission. The reduced size and overlap between home ranges due to lower competition for food may result in a decrease in conflicts between individuals during the year (Sanchez and Hudgens, 2015). Analyses of data collected using proximity-sensing radiocollars on a population of devils at high density prior to DFTD outbreak showed that bite wound frequency is directly related to the number of partners during the mating season for both sexes (Hamilton et al., 2017). With the rapid decrease in density following DFTD outbreak and the observed higher spatial segregation, the cost of finding a partner in long diseased populations increased. Sexual selection should then favour males investing more energy into single mating events and females becoming less selective in the choice of a partner (Lamb et al., 2017). Such changes in social behaviour may then challenge the otherwise highly frequency-dependent transmission of DFTD (Sah et al., 2017) by reducing the frequency and intensity of biting behaviour. In addition, with higher food resources, subadults grow faster and can therefore mate in their first year instead of their second year as commonly observed in heathy populations (Lachish et al., 2009). An increase in precocious breeding could explain the stability of the subadult densities over time. A lower transmission rate of the disease and an increase in local recruitment could explain the devil population persistence observed in long diseased areas.

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CHAPTER 4: Cancer on the move, the effects of a transmissible cancer on the movements of the Tasmanian devils.

"Not all those who wander are lost"

J.R.R. Tolkien

4.1. Introduction

Animals exhibit plasticity in movement that reflect decisions to optimise their behaviour given external stressors (Fortin et al., 2015) and resources in heterogeneous landscapes that are patchily distributed in space and time. How organisms move therefore directly influences their performance or capacity to find enough energy to meet their internal requirements while competing with other organisms (both intra and inter-specific) for access to resources (Clobert et al., 2009; Morelle et al., 2015). Stressors include biotic factors such as host-pathogen interactions, and predation which induces vigilance, or abiotic factors, such as temporal changes in resource availability or harsh climatic conditions which can trigger migration events. Individual hosts can also develop sickness behaviours, an adaptative response to an infection, often resulting in reduced movement activity such as lethargy, somnolence and anorexia (Franz et al., 2018) to save energy for the immune system to fight the pathogen. Another cause for behavioural changes in host behaviour is pathogen manipulation, an increase or decrease of host activity induced by the pathogen to facilitate its transmission (Scott, 1988; Lopes, 2014). While the effects of parasites and infectious diseases on wildlife behaviours are widely documented, studies on the effects of cancer on wildlife behaviour are very limited, and are nonexistent for movement ecology (Vittecoq et al., 2013).

Wildlife cancer has long been considered as a rare, post-reproductive disease linked to senescence, genetic diversity and inbreeding (Nagy et al., 2007; Ujvari et al., 2018). Recent studies, though, suggest that cancer in wildlife has an important role for animal ecology and evolution (Thomas et al., 2017), which affects all multicellular organisms (Vittecoq et al., 2015). Cancer detection in wildlife is complicated, unlike in humans and domestic animals, due to the difficulty of accessing sick or dead individuals and a lack of field-based diagnostic tools (Wobeser and Wobeser, 1992). In addition, when a more direct cause of mortality (e.g. predation, trauma) is identified, generally no post mortem analysis is done (Martineau et al., 2002) and any information on cancer is lost. Prevalence and incidence of cancer in wildlife is therefore very difficult to estimate, but recent interest for wildlife cancer epidemiology in Santa Carolina Island foxes (Vickers et al., 2015), fish populations (Coffee et al., 2013), Tasmanian devils (Margres et al., 2018) and molluscs (Metzger et al., 2016) have highlighted the role of oncogenic processes in ecosystem function and animal ecology and conservation (McAloose and Newton, 2009; Kareva, 2011; Vittecoq et al., 2013; Madsen et al., 2017).

As a clonal multiplication of malignant cells, cancers have high metabolic rates and compete for energy and nutrients from the host's budget (Ryan et al., 2007), likely triggering behavioural changes in the host. Such behaviours are difficult to observe empirically, but since the mid-1990's the spread of the devil facial tumour disease (DFTD) (Hawkins et al., 2006) has provided a unique opportunity to study behavioural changes associated with cancer (Pesavento et al., 2018). Infected devils typically have tumours around the mouth and the face resulting in the death of the animal within 6 to 12 months from the first visual symptom (Hamede et al., 2012), by metabolic exhaustion, metastases and mechanical impairment of feeding (Loh et al., 2006). The high mortality of DFTD has and is still causing rapid collapse in the population density of Tasmanian devils (Hawkins et al., 2006; Lazenby et al., 2018) and inducing life history changes (Jones et al., 2008; Lachish et al., 2009) with unknown consequences on the individual movement behaviours of Tasmanian devils. Considering the heavy burden of tumours and their reliance on direct contacts between hosts for transmission (Hamede et al., 2013), individual plasticity in movement behaviours is expected to play an important role in the evolutive race between DFTD and devils.

Direct physical effects of tumours on their hosts have been described in wild and captive populations of the western barred bandicoot (Woolford et al., 2008) and in green sea turtle populations (Chaloupka et al., 2009). DFTD tumours occur predominantly on the face (Hamede et al., 2013), with only a few cases documented on the body and legs so are unlikely to affect locomotion directly. Although assimilated to a parasitic infection (Ujvari et al., 2016), there is no evidence of DFTD manipulating the behaviour of its hosts in the way, for example, that the fungal parasite, *Ophiocordyceps kniphofioides*, drives infected ants to bite onto vegetation just before being killed by the fungus (Andersen et al., 2009). We hypothesize that devils with DFTD will optimize their foraging strategies by reducing the energy allocated to movement to compensate for the additional and increasing metabolic costs of cancer progression. Because movement decisions are made at different spatio-temporal scales, we analyse different movement behaviours that are relevant to four temporal scales: seasonal and weekly home ranges, relative and absolute daily distances, and movement activity every fifteen minutes. We compare these behaviours between healthy and diseased adult devils from the same population, that were tracked at the same time.

4.2.Methods

4.2.1. Study sites and tracking data

The Freycinet peninsula (FNP) is a narrow strip of land (300 km^2) protruding from the central east coast of Tasmania, Australia (42°03’53’’S, 148°17’14’’E) (Figure 1). Estimated devil density at the beginning of the study (2015) was 0.22 devils/ km2, compared to 0.60 devils/ km^2 in 2001 when the first case of DFTD was identified (Chapter 2 of the thesis). Based on camera trap data along a 2 km transect (14 cameras for 39 days), the total available prey biomass (wallaby=15 kg and Tasmanian pademelon = 5 kg) during the survey was 1217.5 kg (Cunningham, pers comm). The peninsula is characterised by a rugged spine of sandstone and granite mountains (up to 620 m asl), with flat areas to the west around a large tidal lagoon, and to the north, along the Apsley river. The peninsula is dominated by dry eucalypt forests, with a mosaic of native grassland to the west and heathland along the coast. The northern area is mostly private farmland with large areas of pasture supporting cattle. The average monthly temperature range between 9 and 18°C, with an annual average rainfall of 690 mm.

Between August and October 2015 and 2016, GPS tracking devices were fitted on eighteen resident adult Tasmanian devils in Freycinet peninsula, five of which presented clinical symptoms of DFTD (Table 1). The animal position was recorded every fifteen minutes between 17:00 and 7:00. The tracking data was checked and cleaned following (Andersen et al., 2017), the list of all devil tracked is available in Appendix S1.

Figure 1: Study area

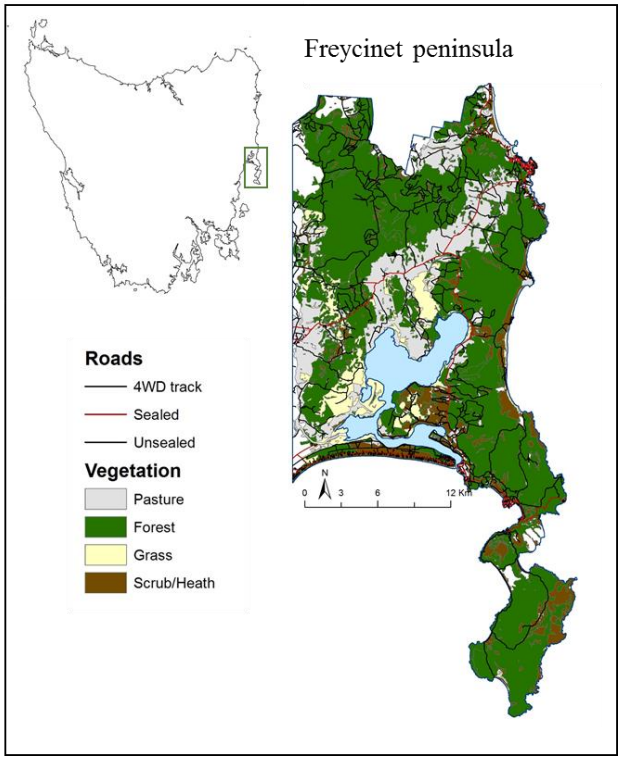
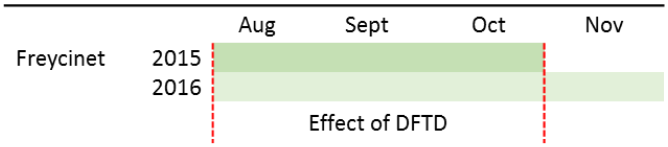


Table 1: sample sizes for each analysis. The effect of DFTD was measured with tracking data from Freycinet only, restricted to the months of August, September and October, between 17:00 and 7:00).



		Effect of DFTD (17:00 – 7:00)	
		Healthy	Diseased
Females	Seasonal home ranges	9	3
	Weekly home ranges	462	139
	Total nights	510	157
	Total steps (15 min)	10722	2519
Males	Seasonal home ranges	4	2
	Weekly home ranges	172	34
	Total nights	196	43
	Total steps (15 min)	4799	419

4.2.2. Seasonal and weekly home ranges

For the seasonal home range, we used the Biased Random Bridges (BRB) approach to estimate utilization distributions for each individual based on all GPS locations (Benhamou, 2011). The selection of this methods was based on its capacity to deal with spatial and temporal autocorrelation derived from the high frequency tracking design (every 15 minutes). In addition, BRB allows for better management of gaps in the data as a result of no location recorded during day-light hours. Home range sizes were then calculated by movement-based kernel density estimation (MKDE) on the 95% utilisation distributions (Benhamou and Cornélis, 2010). Once home ranges were estimated, we used a generalized linear model approach (GLM) to measure the association of sex and DFTD with the home range size. We applied a model selection based on the Akaike Information Criteria corrected for small sample size (AICc) (Burnham and Anderson, 2002). The list of model formulations assessed, and parameter estimates for the best model are presented in Appendix S2a. Calculations and model fitting were done in R (2018, version 3.5.2) with the package "adehabitat".

With the same method, we calculated weekly ranges for each animal as a proxy to the area necessary to provide food. We sub sampled the tracking data using a moving window of 6 days with one day increment (days 1 to 6, days 2 to 7 … days n to n+5). For each weekly dataset, we then calculated the 95% MKDE area. We log transformed the home range sizes to fit a linear mixed model with sex and DFTD as fix effects and ID as random effect to account for the repeated measures per individual devils. The list of model formulations assessed, and parameter estimates are presented in Appendix S2b.

4.2.3. Daily movement

We divided the daily movement of devils in two distance metrics. Firstly, we measured the total distance moved every night by summing the linear distances between each GPS location. Secondly, we measured the linear distance from the first location of the night to the last location to estimate a daily drift as a proxy for the fidelity of devils to particular denning sites. We log transformed the response variables to fit linear mixed models with sex and DFTD as fix effects and ID as random effect to account for the repeated measures within individual devils. The list of model formulations assessed, and parameter estimates are presented in Appendix S2c+d.

4.2.4. Hourly activity

We used hidden Markov models (HMM) on devil trajectories to estimates behaviour states based on the distribution of step length and turning angles of all individuals (Michelot et al., 2016). We only considered a step when location fixes were 15 minutes apart to standardize the behaviours across all animals (Langrock et al., 2012). We tested the effect of site, sex and DFTD on the transition probabilities associated with the movement states. Following Pohle et al. (2017), we restricted the possible number of states to two or three, representing biologically relevant behaviours. We only report on the three-state models as they systematically performed better than the two-state models, consistent with recent studies on wild carnivores (Ellington and Gehrt, 2019; Rio-Maior et al., 2019). We selected the best model based on the AICc value, and then assigned each animal location its most probable behaviour state using the Viterbi algorithm on the best model (Zucchini et al., 2016). The list of model formulations assessed, and parameter estimates are presented in Appendix S3.

We then estimated the probability of an individual to be in each state at a given time during the night (every 15 minutes) using a multinomial generalized additive mixed modelling (GAMM) approach. The GAMM formulations provide the flexibility to account for non-linearities in the patterns of behaviours along the night. This non-linearities can be assessed by the values of effective degrees of freedom for the smooth terms. Values close to 1 support a linear relationship between variables while values above 1 suggest a strong non-linear relationship. We assessed the effect of DFTD on each sex by fitting the GAMM formulation using male and female data independently. Predictor variables included day of measurement, time and their interaction with DFTD as fixed terms, while individual ID was included as a random effect. Day, and time were modelled as cubic regression splines with their interaction modelled as a tensor product (t2). The interaction with DFTD was included using the 'by' term within the spline specification (Wood, 2017). All calculation and model fitting were done in R with the packages "moveHMM" and "mgcv". The model formulation and parameter estimates are presented in Appendix S2e.

4.3. Results

4.3.1. Seasonal and weekly home ranges

We could not detect any effect of DFTD or sex on the seasonal home ranges (August to October) in Freycinet, the best model was the Null model showing a mean seasonal home range size of 21.7 km^2 (CI95%:16.7-26.7). At the weekly scale, the best model included the interaction term sex*month. Females showed stable weekly range sizes in August and September and significantly increased their roaming in October. Inversely, males significantly reduced their weekly home ranges between August and September and then remained stable in October (Figure 2). Overall, males were using bigger weekly home ranges than females. There was no support for any influence of DFTD on the weekly home ranges.

4.3.2. Daily movement

The best model explaining the average distance moved every night in Freycinet was the Null model, directly followed by the model with DFTD (ΔAICc = 2.01). Due to the limited sample size, the trend associated with DFTD may be due to confounding factors and only explain 20% of the variance. We therefore did not detect any effect of the tumours on the daily distance moved in our study. The best model explaining the daily drift in Freycinet included the interaction term sex*month. Females showed a strong fidelity to their den (Figure 3) during each month. Males, on the other hand, showed a continuous decrease in their daily drift from August to October and a globally much lower den fidelity than females. No effect of DFTD was observed on the daily drift.

Figure 2: Average weekly home ranges (6 days) for male and female devils in Freycinet. Areas measured as 95% movement-based kernel density estimator (MKDE). The black bars represent the standard error.

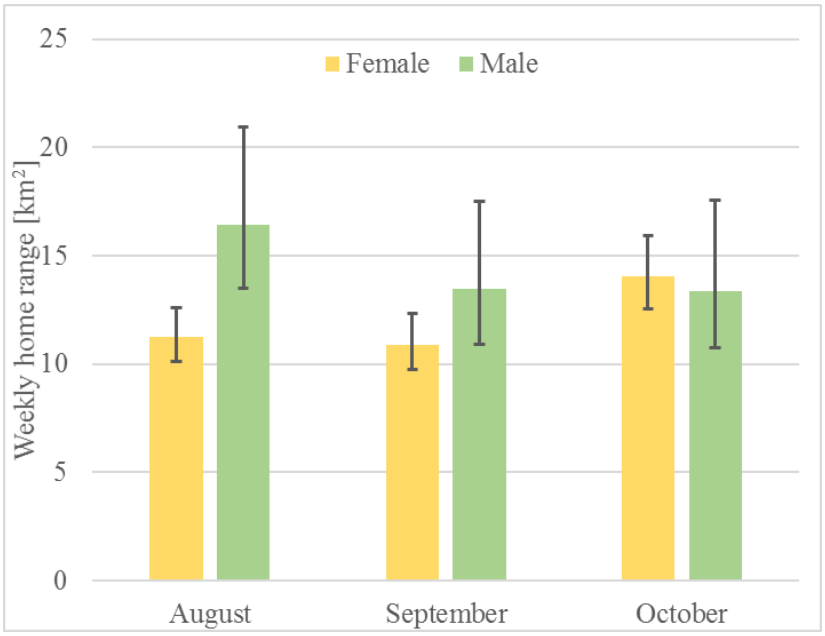
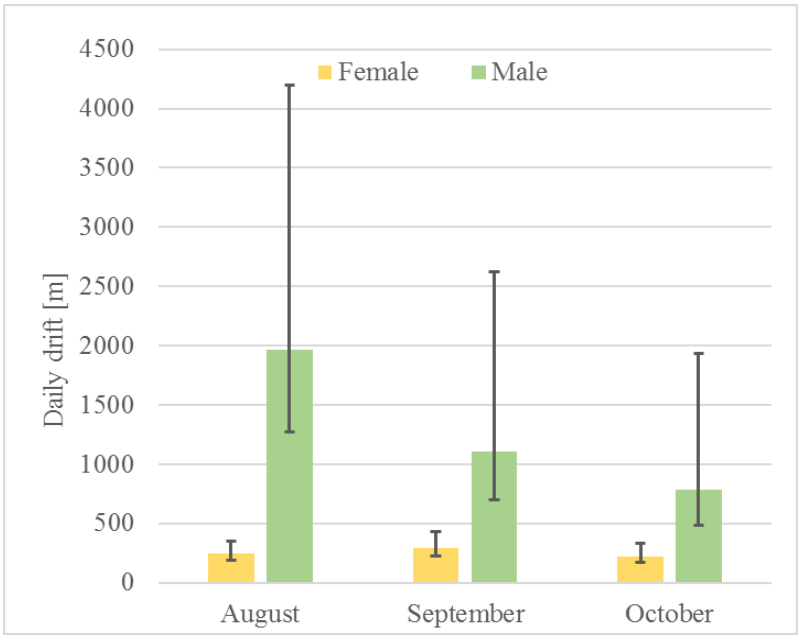


Figure 3: Average distance moved per night for male and female devils in Freycinet. Distance measured as the sum of the linear distances between tracking locations. The black bars represent the standard error

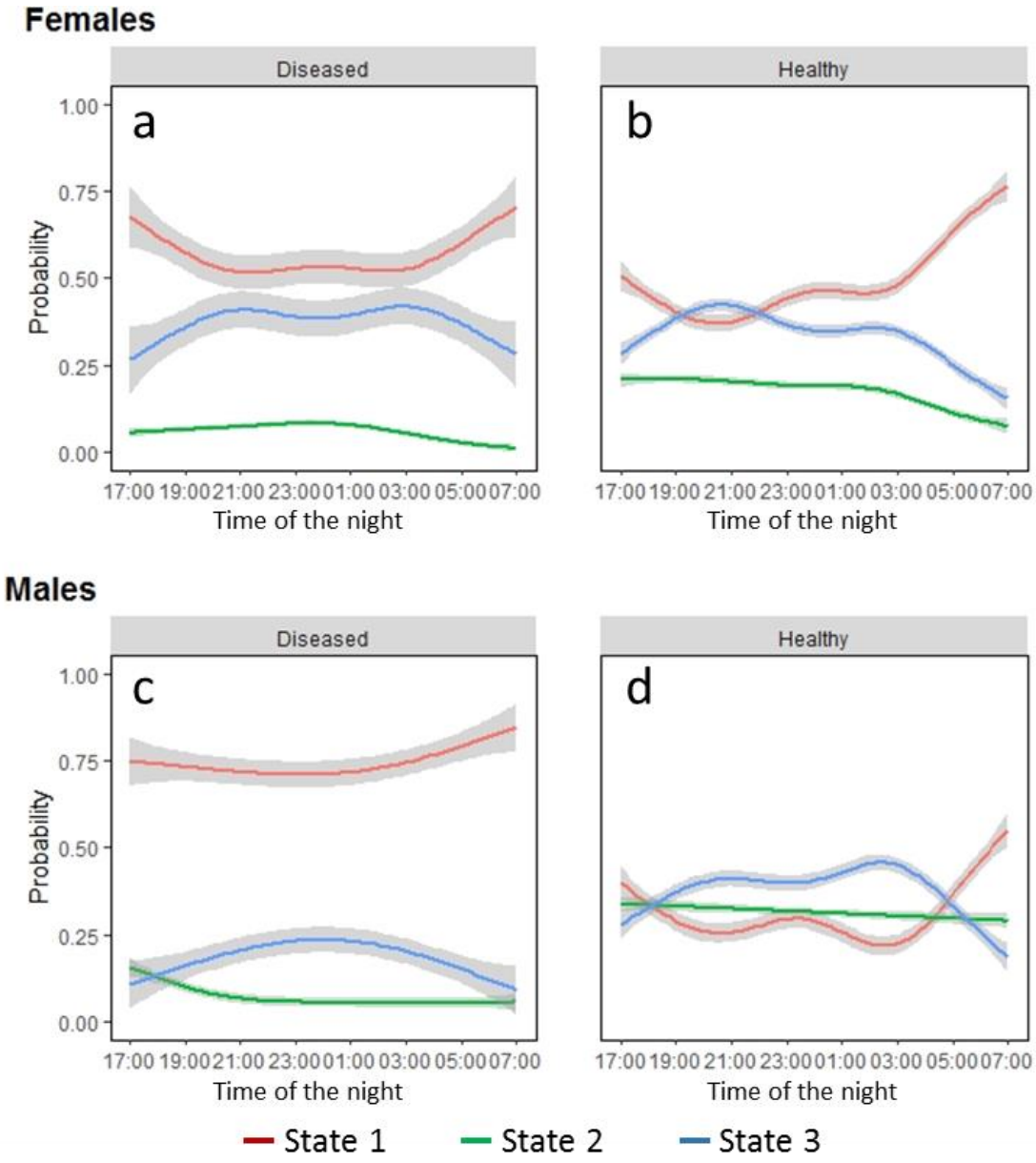


4.3.3. Hourly activity

The best HMM model based on the tracking data showed three behavioural states with transition probabilities best explained by the site, sex and DFTD. The “state 1” represents a quasi-absence of movement (mean step length: 11.4 meters SD10.0) and a wide distribution of turning angles centred on 3.09 rad (concentration: 0.58). The “state 2” can be described as a slow, erratic movements defined by small steps (mean step length: 197.9 m SD204.2) and a very wide distribution of turning angles (mean: 0.01 rad, concentration: 0.30). The “state 3” suggest faster directional movements with longer steps (mean step length: 614.7 m SD273.4) and a narrow distribution of turning angles centred on -0.02 rad (concentration: 2.15) (Appendix S3).

Compared to healthy animals, females with DFTD showed a decrease in activity during the night (higher probability to be in movement state 1). This was mostly compensated by reducing the slow erratic movements (state 2), which decreased from more the 25% to less than 10% through the night, while long directional movements (state 3) were maintained (Figure 4a+b). Compared to females, healthy males were globally more active, with more time spent in state 2. When infected by DFTD, males showed a stronger change in activity than females, both movement behaviours (states 2 and 3) dropped (Figure 4c+d) with males spending more than 75% of the time stationary (state 1).

Figure 4: Average activity in Freycinet during the night (every fifteen minutes between 17:00 and 7:00) based on the probability of being in one movement state as modelled by HMM. The curves represent the smoothed averages across the night with standard error (grey areas) for state 1, red: stationary, state 2, green: slow erratic movements and state 3, blue: fast directional movements. The probabilities were modelled independently for each sex with the effect of DFTD: healthy females (a) vs diseased females (b) and healthy males (c) vs diseased males (d).



4.4. Discussion

We measured the changes in movement pattern associated with cancer in wild Tasmanian devils. By using GPS tracking devices on devils during the epidemic of a transmissible cancer, including diseased individuals, we present the first empirical evidence of changes in movement behaviours associated with cancer in wildlife. Females and males showed very different pattern of movement behaviours across all scales, which reflected on the impact of DFTD. Globally reducing the daily activity of the hosts, the effect of DFTD was much stronger for males than females who maintained their fast, directional movements. The movement behaviour from a naïve population suggest a potentially stronger impact of DFTD on males than females at the time of first emergence. These sex-biased changes in behaviour support the higher ability of females to cope with the cancer (Ruiz-Aravena et al., 2018). Our study represents the first attempt to measure the effect of cancer on wildlife movement. The small sample size and tracking time in our study being strong limiting factors, especially considering the progressive nature of cancer, our results should be considered as a stepping stone for future research.

For most species, movement behaviours are strongly linked with reproduction and foraging, part of which parental care represents a major energetic cost for adults (Boonekamp et al., 2014). Different strategies have evolved in nature ranging from cooperative groups in meerkats (Clutton-Brock et al., 2001) to shared parental duties in red foxes (Malcom, 1985) and solitary maternal care in cheetahs (Caro and Collins, 1987). Tasmanian devils follow the latter, with females assuming parental care alone (Pemberton, 1990) resulting in resource driven movement decisions (Saïd et al., 2009). The tracking data used in our study covers the time during which females have dropped their young in a den (after four months in the pouch) but are still actively feeding them (Guiler, 1970) until the young start to find food on their own. Although moving the same distance per night than males, the necessity to come back to the same den every night explain their smaller weekly home ranges and daily drifts. It may also influence females to spend more time in rapid directional movements to reach feeding grounds with little time spent in small erratic movements.

Based on optimal foraging theory (MacArthur and Pianka, 1966), this pattern of movement suggest that females follow an "energy maximizer" strategy (Schoener, 1971; Charnov, 1976) meaning that foraging is limited by time and that the organism should opportunistically take as much food as it can from each foraging event. Male spatial ecology on the other hand is driven by both resources and social dominance (Clapham et al., 2012). While females use a single den when they have large pouched or denned young, males and females outside this breeding period use multiple dens (Pemberton, 1990). The larger daily drift observed in male devils explain their larger weekly home ranges, while moving the same distance. Globally more active than females, males spend particularly more time in slow erratic movements suggesting a "time minimizer" foraging strategy. The faster the energy requirements are met, the more time the animal can spend on maintaining its dominance.

Devils with clinical signs of DFTD showed a reduction in movement activity during the night, more accentuated for males than for females. This reduction in movement may allow individuals to save energy that can be reallocated to immune functions (Lopes et al., 2014). This behaviour has been associated with vector born parasites and cancer in humans (Kumar et al., 2004; Holmstad et al., 2006) and with captive felids (Harrenstien et al., 1996) but never before with cancer in free roaming wildlife. In the case of devils, this lethargy may be associated to the direct drain of energy from the growing tumour tissue (Wright et al., 2017), from the activation of immune response (Pye et al., 2016), or as consequence of bioactive products from the tumour metabolism (Biancur et al., 2017). In our study, DFTD exacerbates the movement decisions of diseased males toward a strategy of minimizing movement. For them, body condition has been described to decrease up to approximately 30% with tumour growth which may equate the cost of reproduction (Ruiz-Aravena et al., 2018). In this condition, moving may increase the general rate of decay of infected males. The reduced activity in infected males may also reduce their contact with conspecifics (Owen-Ashley and Wingfield, 2006; Hennessy et al., 2014) which could in turn affect the transmission of the tumours (Hamede et al., 2009). Females with cancer alter their movement strategy by reducing the slow erratic movements during the night but maintain their fast, directional movements. This suggests that diseased females may optimize the energy intake by opportunistically gathering food while commuting between food patches and their den.

Because foraging is necessary for the survival of the dependent young, higher tolerance to the cancer may therefore increase the fitness of females, allowing them to maintain a better body condition relative to males at equal tumour volume (Ruiz-Aravena et al., 2018). If the metabolic costs of the cancer become too high, females can compensate by reducing the number of young in the den to maximize the survival of the remaining ones (Scott, 1988; Balme et al., 2017). Larger litter sizes at birth (Lazenby et al., 2018) and females biased sex ratio (Lachish et al., 2009) in devil diseased populations therefore add to the long-term fitness of the population (McDonald et al., 2016).

Movements are essential for the fitness of an organism and therefore must be resilient to external stressors. The mechanical capacity of an animal to move is the result of a long evolutionary process and should reflect the optimal way of going from point A to a point B. Understanding this mechanism is important, but it is unlikely to change within the life span of the organism. What is under selection is the actual decision of moving and the pattern of movement used along the path. These decisions are motivated by internal and external factors influencing the organism at different scales, creating a multilevel pattern of movements. If the scale of observation is too broad, minor or short-term changes in movement could be missed. In our study, we could only measure an influence of DFTD on the daily movements and on the activity pattern, based on 15 minutes steps. Any observation at a weekly or monthly scale would have concluded on the absence of changes associated with DFTD. Yet, observing only the fine scale movements may not be enough to understand the true motivations underlying the observed pattern. Without assessing the movement patterns at larger scales, we wouldn't have understood the potential link between parental care, foraging strategies and movement response to DFTD. Additional data are necessary to confirm our observations and to test for a seasonal effect while longer tracking time could inform on the influence of the tumour growth on the movement decisions. Using GPS collars in Arthur River during the outbreak could provide the opportunity to measure the impact of DFTD at different stage of population density. Our study showed that today's GPS technology is sensitive enough to observe the impact of pathogens on host movement behaviours, and that a multiscale framework is necessary to understand the implications of the changes on the spatial ecology of the host.

The majority of cancers in wildlife are not transmissible but may be triggered by viruses or chemical pollutant (Pesavento et al., 2018). The evolution dynamics in these cases is intimately linked to the individual capacity to tolerate and resist the progression of the tumour. Individual heterogeneity in movement behaviours can provide a support to develop sickness behaviours in response to cancer, as described for many pathogens (Franz et al., 2018). Integrating the concepts of spatial ecology at different scales allow to measure and predict this individual heterogeneity which could then be integrated in epidemiological models (Dougherty et al., 2018) to improve the long-term predictions outcome of infectious diseases.

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4.6. Appendix S1

Tracking summary of Tasmanian devils in Freycinet

collar	Name	sex	dftd	year	start	end	days	attempt	fixes
FNP001	mcsteamy	m	1	2015	12/08/2015	1/09/2015	20	422	223
FNP002	hodor	m	1	2015	12/08/2015	22/09/2015	41	909	485
FNP003	psycho	f	1	2015	7/08/2015	11/10/2015	65	1336	630
FNP004	tulip	f	2	2015	11/09/2015	31/10/2015	50	1071	456
FNP005	mcsteamy	m	1	2015	11/09/2015	15/10/2015	34	762	405
FNP006	dumont	f	1	2015	13/08/2015	10/10/2015	58	1290	711
FNP007	cheryl	f	1	2015	13/08/2015	23/10/2015	71	1459	746
FNP008	petal	f	2	2015	26/08/2015	30/10/2015	65	1394	736
FNP009	crixus	m	2	2015	11/09/2015	24/09/2015	13	279	115
FNP011	dolmades	m	2	2015	10/08/2015	11/09/2015	32	690	304
FNP013	progress	f	1	2015	5/08/2015	13/10/2015	69	1364	658
FNP015	sanza	f	1	2016	25/08/2016	7/10/2016	43	2408	1373
FNP016	bluebell	f	1	2016	3/09/2016	27/10/2016	54	2544	1919
FNP017	jonsnow	m	1	2016	24/08/2016	19/11/2016	87	4816	3284
FNP018	progress	f	1	2016	3/09/2016	4/10/2016	31	1392	689
FNP019	flower	f	2	2016	26/08/2016	7/10/2016	42	2296	1327
FNP020	robstark	m	1	2016	2/09/2016	5/10/2016	33	1535	1114
FNP022	dumont	f	1	2016	22/08/2016	23/10/2016	62	3472	2389
FNP023	angie	f	1	2016	2/09/2016	9/12/2016	98	4512	3073

4.7. Appendix S2

Appendix S2a: Model selection and parameters for the seasonal home range size of devils in Freycinet. Generalized linear model with home range size (km^2) as response variable and sex (female vs male) and DFTD (diseased vs healthy) as predictor variables. Models are ordered by their AICc value.

Intercept	DFTD(h)	sex(m)	DFTD(h):sex(m)	df	logLik	AICc	Δ AICc	weight
21.67				2	-67.881	140.6	0	0.60
18.32	4.64			3	-67.522	142.8	2.2	0.20
20.90		2.31		3	-67.784	143.3	2.7	0.15
17.23	4.89	2.72		4	-67.383	145.8	5.2	0.04
18.32	3.44	0.001	3.90	5	-67.322	149.6	9.0	0.01

Appendix S2b: Model selection and parameters for the weekly home range sizes of devils in Freycinet. Linear mixed effect model with home range size log(km^2) as response variable; sex (female vs male), DFTD (diseased vs healthy), month (August, September, October) as predictor variables; and animal ID as random factor. Models are ordered by their AICc value.

Intercept	sex(m)	DFTD(h)	month(Sep)	month(Oct)	month(Sep):sex(m)	month(Oct):sex(m)	DFTD(h):sex(m)	df	logLik	AICc	Δ AICc	weight
2.419	0.379		-0.030	0.222	-0.168	-0.429		8	-331.101	678.4	0	0.708
2.310	0.390	0.144	-0.030	0.223	-0.169	-0.432		9	-331.545	681.3	2.93	0.163
2.346	0.299	0.097	-0.030	0.224	-0.169	-0.432	0.130	10	-331.460	683.2	4.81	0.064
2.546			-0.081	0.118				5	-337.048	684.2	5.79	0.039
2.473	0.220		-0.080	0.120				6	-337.105	686.3	7.93	0.013
2.474		0.010	-0.081	0.119				6	-337.627	687.4	8.98	0.008
2.385	0.229	0.116	-0.080	0.120				7	-337.641	689.4	11.04	0.003
2.409	0.167	0.084	-0.080	0.120			0.088	8	-337.574	691.3	12.95	0.001
2.520								3	-350.151	706.3	27.95	0
2.452	0.208							4	-350.294	708.6	30.26	0
2.450		0.096						4	-350.719	709.5	31.11	0
2.367	0.216	0.114						5	-350.820	711.7	33.33	0
2.400	0.130	0.069					0.122	6	-350.708	713.5	35.14	0

Appendix S2c: Model selection and parameters for the daily distance moved of devils in Freycinet. Linear mixed effect model with distance log(km) as response variable; sex (female vs male), DFTD (diseased vs healthy), month (August, September, October) as predictor variables; and animal ID as random factor. Models are ordered by their AICc value.

Intercept	sex(m)	DFTD(h)	month(Sep)	month(Oct)	month(Sep):sex(m)	month(Oct):sex(m)	DFTD(h):sex(m)	df	logLik	AICc	Δ AICc	weight
8.742								3	-1302.92	2611.9	0	0.548
8.566		0.238						4	-1302.91	2613.9	2.01	0.201
8.752	-0.033							4	-1303.60	2615.2	3.39	0.101
8.780	-0.617	-0.036					0.819	6	-1301.73	2615.6	3.70	0.086
8.573	-0.023	0.238						5	-1303.61	2617.3	5.42	0.036
8.844			-0.154	-0.073				5	-1304.48	2619.0	7.16	0.015
8.669		0.236	-0.153	-0.072				6	-1304.48	2621.1	9.20	0.005
8.858	-0.041		-0.156	-0.076				6	-1305.14	2622.4	10.51	0.003
8.898	-0.640	-0.045	-0.159	-0.086			0.837	8	-1303.24	2622.6	10.78	0.002
8.681	-0.031	0.235	-0.154	-0.075				7	-1305.16	2624.4	12.59	0.001
8.874	-0.608	-0.039	-0.149	-0.040	-0.022	-0.210	0.867	10	-1304.14	2628.5	16.67	0
8.650	0.020	0.250	-0.144	-0.032	-0.026	-0.192		9	-1306.16	2630.5	18.65	0

Appendix S2d: Model selection and parameters for the daily drift of devils in Freycinet. Linear mixed effect model with distance log(km) as response variable; sex (female vs male), DFTD (diseased vs healthy), month (August, September, October) as predictor variables; and animal ID as random factor. Models are ordered by their AICc value.

Intercept	sex(m)	DFTD(h)	month(Sep)	month(Oct)	DFTD(h): month(Sep)	DFTD(h): month(Oct)	sex(m): month(Sep)	sex(m): month(Oct)	DFTD(h): sex(m)	df	logLik	AICc	Δ AICc	weight
5.531	2.053		0.166	-0.111			-0.740	-0.810		8	-1506.34	3028.8	0	0.373
6.284	1.455	-0.640	-0.818	-0.779	0.897	0.476				9	-1506.08	3030.4	1.50	0.176
5.507	2.057	0.032	0.167	-0.110			-0.742	-0.812		9	-1506.08	3030.4	1.52	0.174
5.732	1.480		-0.069	-0.349						6	-1510.16	3032.4	3.57	0.062
5.587	1.533									4	-1512.22	3032.5	3.63	0.061
6.009	0.787	-0.368	-0.070	-0.353					0.980	8	-1508.52	3033.2	4.35	0.042
5.829	0.922	-0.323							0.866	6	-1510.66	3033.4	4.57	0.038
5.741	1.479	-0.013	-0.068	-0.349						7	-1509.93	3034.0	5.13	0.029
5.594	1.532	-0.010								5	-1511.98	3034.0	5.17	0.028
6.887		-0.799	-0.857	-0.846	0.938	0.546				8	-1509.93	3036.0	7.18	0.010
6.221			-0.071	-0.358						5	-1514.41	3038.9	10.04	0.002
6.090										3	-1516.69	3039.4	10.57	0.002
6.316		-0.132	-0.071	-0.358						6	-1513.95	3040.0	11.14	0.001
6.188		-0.134								4	-1516.22	3040.5	11.63	0.001

Appendix S2e: Parameters for the daily activity of devils in Freycinet. The models were fitted for females and males, independently. Multinomial generalized additive mixed effect model with movement state (1, 2, 3) as response variable; fix effect was constructed as day + time modelled as a cubic regression splines within a tensor product (t2) and an interaction with DFTD (diseased vs healthy) and animal ID as random factor. Edf=effective degrees of freedom for the smooth terms, a value close to 1 support linear relationship while values above 1 suggest strong non-linear relationships.

Parametric coefficients

	Females			Males		
	Estimate	Std. Error	z value	Estimate	Std. Error	z value
Int_healthy	-1.203	0.032	-37.32	-1.127	0.109	-10.31
Int_diseased	-0.450	0.029	-15.36	-1.335	0.233	-5.73

Approximate significance of smooth terms

	edf	Ref.df	Chi.sq	p-value	edf	Ref.df	Chi.sq	p-value
ID (State2)	10.74	12.00	824.82	0.003	3.73	6.00	281.78	0.387
State2:healthy	14.29	16.11	233.66	<0.001	21.57	24.54	108.40	<0.001
State2:diseased	20.41	25.28	30.55	0.233	9.54	12.10	38.63	<0.001
ID (State3)	10.55	12.00	3085.46	0.017	4.02	6.00	404.66	0.120
State3:healthy	33.06	38.34	371.99	<0.001	29.68	34.33	192.18	<0.001
State3:diseased	24.36	28.70	96.98	<0.001	6.57	8.27	28.11	<0.001

4.8. Appendix S3:

Appendix S3a: Model selection for the definition of the movement states. The tracking data of all individuals were used in the same model formulation. The hidden Markov model was fitted for three movement states. We tested the effect of site (Arthur River vs Freycinet), sex (female vs male) and DFTD (diseased vs healthy) on the transition probabilities between movement states. Models are ordered by their AICc value.

site	sex	DFTD	site:sex	site:DFTD	sex:DFTD	AICc	Δ AICc
+	+	+				461248.8	0
+		+				461307.0	58.2
+	+		+			461310.1	61.3
+	+					461318.1	69.3
+		+		+		461328.2	79.4
+						461384.8	136.0
	+	+			+	461392.7	143.9
	+	+				461420.9	172.1
		+				461491.1	242.3
	+					461505.8	257.0
						461568.3	319.5

Appendix S3b: Estimates parameters for the best movement model. Presentation of the three states with their step length [m] distribution and turning angle distribution [rad].

	state 1	state 2	state 3
Step length	11.410	197.908	615.218
sd	10.040	204.211	273.192
zero-mass	0.022	0.002	>0.001
Turning angle	3.092	0.009	-0.019
Concentration	0.586	0.295	2.150

Appendix S3c: Matrix of transition probabilities between the three movement states from the best model, including site, sex and DFTD as predictor variables.

	1 -> 2	1 -> 3	2 -> 1	2 -> 3	3 -> 1	3 -> 2
Intercept	-4.458	-17.828	-2.853	-0.948	-2.742	-1.560
Freycinet	-0.059	-3.989	0.607	0.356	0.185	-0.387
Male	0.135	-2.150	-0.023	-0.326	-0.007	0.036
Healthy	0.649	-4.766	0.552	0.041	-0.284	0.075

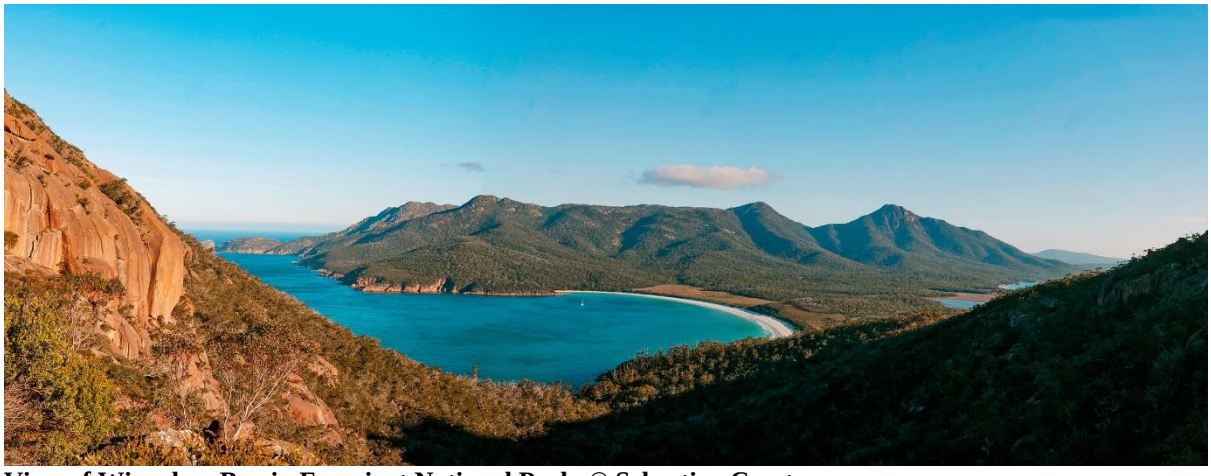
CHAPTER 5: General discussion

"Not all ... wander are lo...

J.R.R. Tolkien

5.1.Research summary

The concept of my thesis emerged from the disparity between the significant epidemiological knowledge on devil facial tumour disease (DFTD), but lack of empirical data on the spatial ecology of its unique host, the Tasmanian devil (*Sarcophilus harrisii*). I articulated my research around a field-based framework integrating the theories of spatial ecology and movement ecology to epidemiology at different scales to measure the impact of DFTD in the long-diseased populations of Tasmanian devils. I compared the movement decisions of devils with clinical signs of DFTD and healthy individuals from the same population, showing scale and sex effects of cancer infection on movement decisions. While no effect of DFTD could be measured on seasonal and weekly home ranges, the presence of tumours was associated with a reduction of movement activity each night, which was more severe for males than females. In addition, comparing movement patterns pre- and post-DFTD outbreak showed that the reduction of devil density caused by DFTD lead to a shift in female spatial organisation towards a more clustered pattern (smaller home range sizes with increased spatial segregation of highly overlapping pairs of home ranges). At a larger scale (north-east corner of Tasmania), the low-density residual devil population (15 to 20 years after DFTD outbreak) displayed a heterogenous distribution with high abundance in the coastal heathland and away from open pastures and high altitudes. My thesis reports on the first tracking data collected in a diseased population of Tasmanian devils, including the very first tracking of individuals with DFTD, and emphasizes the importance of multiscale frameworks to study the epidemiology of wildlife diseases.



View of Wineglass Bay in Freycinet National Park. © Sebastien Comte

5.2.Research outcome

Wildlife disease epidemiology is steadily incorporating concepts of spatial ecology, revealing complex patterns of host pathogen dynamics at different scales. In my thesis, I further develop the concept of spatial epidemiology by integrating movement behaviours in a multiscale framework from individual movement decisions to population spatial organisation and landscape distribution. I used this novel framework to explore the mechanisms underlying the unforeseen resilience of Tasmanian devil populations 20 years after the emergence of the devil facial tumour disease (DFTD). Individual heterogeneity in behaviour as well as sex specific foraging strategies and spatial ecology favour the emergence of an evolutionary response against DFTD. At a larger scale, these changes in spatial organisation, combined with heterogenous resource distribution, shape a pattern of spatial distribution favouring the emergence of a metapopulation dynamics and drive a long-term co-existence between DFTD and devils. The multiscale framework provides empirical evidence of spatially explicit ecological processes across scale potentially enhancing the long-term coexistence of devils and DFTD.

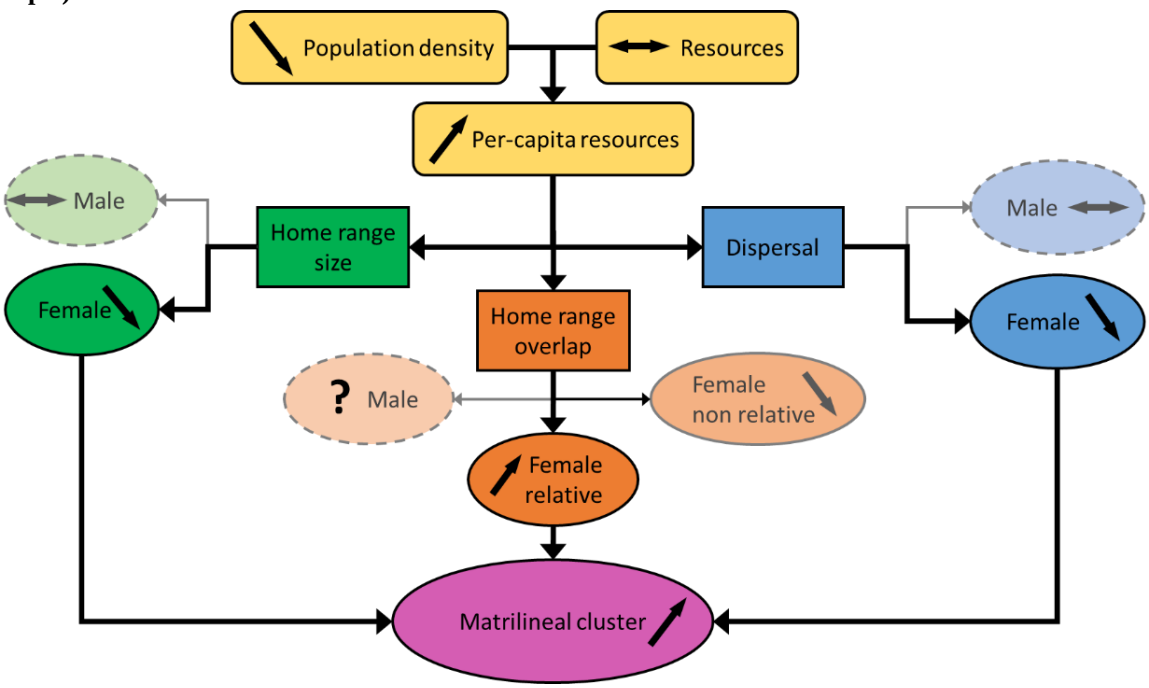
Little is known about the relationship between fine-scale movement decisions and pathogen infections. GPS tracking of host movements is commonly used to assess the risk of exposure of host organisms to a pathogen or to predict the spread of a disease, especially in relation to livestock and human exposure (Kinsley et al., 2019). Individual movements can also inform on the transmission dynamics within a population or a group, especially when associated with contact networks (Craft et al., 2011). Yet, few studies have used tracking devices to directly compare the movements of diseased animals with healthy ones (van Gils et al., 2007), but advances in technology open new perspectives (Kays et al., 2015). Being able to measure the movement of devils at a very fine scale (fifteen minutes) was in fact necessary to observe a response to DFTD infections which was otherwise weak on daily movements and absent at larger scale (week or month home ranges). Using a multiscale array of movements allowed identification of different foraging strategies for males and females reflecting the mono-parental care in devils (males do not participate in raising the young). This led to sex-specific responses to the cancer, possibly suggesting a stronger importance of females in the local persistence of DFTD. Fine-scale GPS tracking is a promising tool to measure sickness behaviours in wildlife, an adaptative response to a pathogen, for species difficult to observe in the wild.

Individual movement strategies scale up to shape the spatial organisation of a population, influencing the contact pattern between hosts and eventually the pathogen transmission. This is probably the most studied scale in wildlife epidemiology benefitting from extensive knowledge on population dynamics (McCallum et al., 2001). The spatial organisation of a host population (relative placements and sizes of individual home ranges) is usually considered as a static factor used to inform or model the transmission dynamics of pathogens (Cooch et al., 2012). Yet, the emergence of a pathogen is almost always associated with changes in host density that influence the spatial and social organisation of the population (Efford et al., 2016). In the case of diseases with a high mortality rate, like DFTD, the decrease in density results in higher resources per capita for the hosts.

As observed with the fine-scale GPS tracking, males and females follow different foraging strategies which influence their spatial response to increased resource availability. In fact, male home range size did not change in the DFTD-induced low density population, but the female spatial pattern did. Female home range sizes became smaller and their relative placement in the landscape shifted toward a more structured pattern with pairs of females showing high overlapping but spatially segregated from other pairs of females. The age difference observed within the pairs suggest that these females may be related, a common structure in mammal populations with young females staying closer to the parental home range (Soderquist and Lill, 1995; Fattebert et al., 2016) while males disperse further to avoid inbreeding (Lawson Handley and Perrin, 2007).

This pattern of matrilineal clusters (Figure 1) may expand beyond the population scale due to reduced dispersal of females but not males in long-diseased areas (Lachish et al., 2011). Recently, Holmala et al. (2018) identified female kin clusters in Eurasian lynx population in Finland; a similar approach could be used on the multiple tissue samples of female devils available across the species range. If this pattern is confirmed and considering that females seem to play a major role in the local persistence of the cancer, maybe male movements, less spatially limited, could be responsible for the spread of the cancer at larger scale (Daversa et al., 2017). To test this hypothesis, we need to set GPS collars on male and female devils during the whole year and, ideally, on dispersing subadults.

Figure 1: Conceptual flow chart leading to the emergence of matrilineal clusters in the population. The black arrows show the trends associated with the DFTD outbreak. The yellow boxes show the consequences of DFTD on the population resulting in cascading effects on home range size (green), home range overlap (orange) and dispersal (blue), three mechanisms potentially leading to matrilineal clusters (purple).



Dispersal and transient movements (exploratory behaviour outside the normal home range) both depend on interindividual interactions (local density and spatial organisation) and the pattern of bioclimatic factors in the landscape. The spatial organisation, also influenced by resource distribution and population density, will define who is leaving and when and the probability of settling down in a new place, while the distance and the path depend on the landscape connectivity (Naidoo et al., 2018). Mapping the spatial distribution of the host in a heterogenous landscape is therefore essential to understand the spatial spread of a pathogen (Becker et al., 2018). Occupancy models provide robust estimates of the occurrence of a species at the detector site but its prediction may be affected by the grain (distance between detectors) (Steenweg et al., 2018) and the spatial scale at which the landscape is sampled (buffer size around the detector) (Viana and Chase, 2019). Using three surveys of devils with different grain, I establish empirical evidence of the effect of the survey design on the predicted occupancy, using the same habitat covariates in the same areas. I also confirm the importance of the spatial scale at which the landscape is sampled and go further by showing that the effect size is specific to each habitat covariate. Integrating these concepts into wildlife surveys will improve the accuracy of future species distribution models.

Based on my spatial predictions, devil abundance in the long-diseased area of the north-east is highly heterogenous with hot spots localized in the coastal complexes and low altitude forests while high steep rugged areas and open pastures were avoided. The heterogenous abundance in the landscape strongly suggests the emergence of a meta-population dynamics which could create a mosaic of local extinction and recolonization desynchronizing the epidemics and the dispersal of the hosts (Fox et al., 2017), improving the long-term survival of the whole meta-population (Siska et al., 2018). Additional large-scale surveys added to the existing monitoring programs (spotlight counting, live trapping and camera traps) will be necessary to predict the distribution of devils over the whole island of Tasmania, characterized by strong climatic and topographic gradients. Integrating genetic information from the host and the tumours into the metapopulation structure represents the next challenge at this spatial scale.

The multiscale framework presented here opens new perspectives for the study of host-pathogen systems by increasing our understanding of individual heterogeneity in host populations. Both spatial ecology and movement ecology are articulated along scaling processes with the finality of understanding the individual heterogeneity in spatio-temporal distribution (Holmes et al., 1994; Allen and Singh, 2016). If the general aim of both spatial and movement ecology is the same, the processes underlying the final patterns are fundamentally different. Spatial ecology has a hierarchical approach on natural ecosystems, with the larger scale patterns influencing and limiting the ecological processes happening at smaller scales (Azaele et al., 2015). Movement ecology on the other hand is an iterative process based on the accumulation of individual decisions over time (Fleming et al., 2014).

Integrating the two disciplines in the same frameworks has two main advantages. First, the spatial and temporal range of scales that can be observed is substantially larger than what any of the two discipline could do alone. Movement decisions can now be recorded almost continuously and in real time but are often restricted to a small sample of the population which make it difficult to inform on the larger spatial scales. There, remote sensing technologies used in spatial ecology gives access to high definition geo-climatic and species occurrence data over the whole planet, but at smaller scales, this information is generally based on successive snapshots, missing some fine scale dynamic processes. Second, due to their specific scaling processes, concomitant observations from the same individuals may follow different patterns based on either spatial or movement ecology, offering a more

complex structure to group individual hosts. Given two hypothetical organisms with an identical profile (female, adult, healthy), their risk of exposure to a pathogen could be spatially informed by the distance to a river for example. But then, at the same distance from the same river, if one organism is moving slowly and the other one is moving fast, their individual risk of exposure may be different. This is the fundamental concept of individual-based modelling which has revolutionised the field of epidemiology by accounting for individual life history and epidemiological state in host populations (Papkou et al., 2016; Malishev et al., 2018; Wells et al., 2018). The multiscale framework presented in my thesis adds a new layer of individual heterogeneity that can be incorporated into future epidemiological research.

The multiscale framework can easily be transposed to more complex host-pathogen systems. As fascinating and novel as DFTD is, it is a relatively simple system with only one host species and a transmission route by physical contact between the hosts. Some pathogens need multiple host species to fulfil their lifecycle, for example adult *Echinococcus multilocularis* worms live in the intestines of wild and domestic canids and shed their eggs in the environment with the faeces of the host (Guislain et al., 2008). The eggs are eventually eaten by small rodents and migrate to their liver in a larval stage waiting the rodent to be preyed upon. In this system, mapping the spatial distribution of the different hosts can reveal the areas of co-occurrence necessary to maintain the life cycle of the parasite (Liccioli et al., 2015). Tracking the movements of the hosts could inform on the fine-scale interactions between the host species and eventually detect individual behaviour affecting the transmission or distribution of the pathogens which could reveal the presence of super-spreader hosts for example (Wong et al., 2015). Vector borne diseases present a different challenge because today, it is still challenging to track the individual movement of insects and other arthropods. So far, multiscale approaches should still consider the distribution of the vectors as a spatially heterogenous risk of exposure and correlate that with the movement pattern of the different hosts (Abad-Franch et al., 2010). This framework would be particularly well suited to studying the dynamics of infectious diseases at the interface of wildlife and domestic animals (both pets and livestock). Modelling the movements and distribution of livestock is much easier than wildlife and can be manipulated to test the robustness of the observations (Böhm et al., 2009). These are just some examples of how spatial ecology and movement ecology can be integrated in epidemiological studies using multiscale designs.

Limited resources may be a restriction in designing and implementing multiscale surveys, especially over large areas. New technologies and data sharing can provide cost-effective solutions. To take full advantage of the framework, it is important to provide quality information at different spatial and temporal scales, implying spatial surveys and animal tracking over several years. Only a few study systems globally benefit from comprehensive datasets, such as the badger population at Woodchester Park in the UK, which is naturally infected with bovine tuberculosis and has been intensively monitored for more than forty years (McDonald et al., 2017). As described previously, tracking devices are becoming smaller and cheaper, and camera traps can reduce the cost of large-scale surveys. But the major change in the last twenty years is the emergence of web-based data repositories covering all ecological fields, from bioclimatic records, to habitat maps, species occurrence, animal tracking and even DNA sequences. Relatively common for human diseases, online data on wildlife diseases are becoming more accessible and more inclusive of citizen science contributions. With this surge of available information, multiscale designs will certainly become the norm in ecology and epidemiology with the necessity to integrate multidisciplinary disciplines in research.

"-Have you thought of an ending?

-Yes, several, and all are dark and unpleasant.

-Oh, that won't do! Books ought to have good endings. How would this do: and they all settled down and lived together happily ever after?

-It will do well, if it ever came to that.

-Ah! And where will they live? That's what I often wonder."

J.R.R. Tolkien

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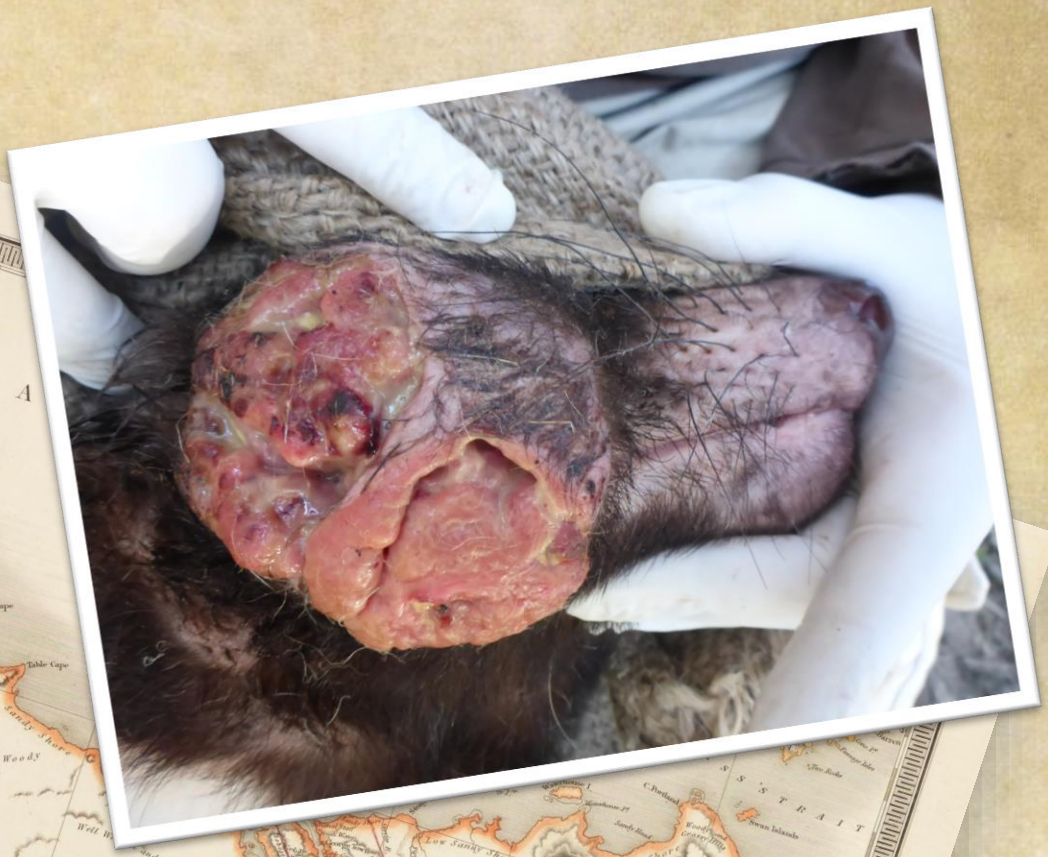
APPENDIX I: Large-effect loci affect survival in Tasmanian devils (*Sarcophilus harrisii*) infected with a transmissible cancer.



wander are lost"

J.R.R. Tolkien

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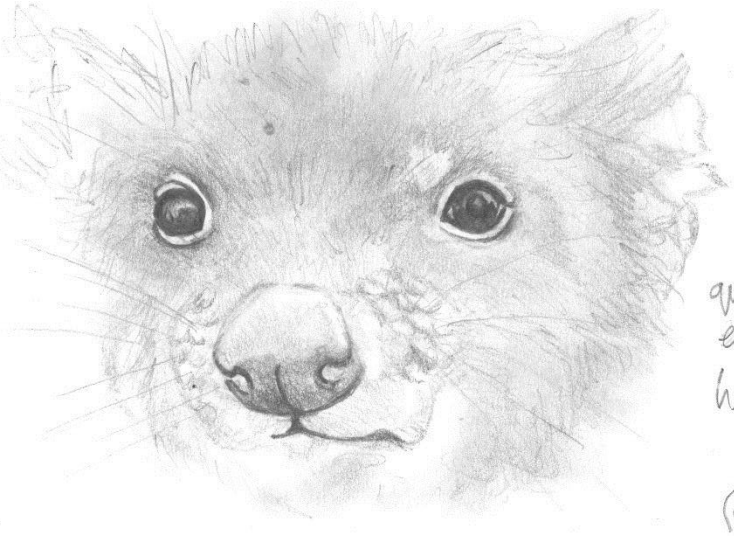
It has been published as: Margres, M. J., Jones, M. E., Epstein, B., Kerlin, D. H., Comte, S., Fox, S., Fraik, A. K., Hendricks, S. A., Huxtable, S., Lachish, S., Lazenby, B., O'Rourke, S. M., Stahlke, A. R., Wiench, C. G., Hamede, R., Schönfeld, B., McCallum, H., Miller, M. R., Hohenlohe, P. A., Storfer, A., 2018. Large-effect loci affect survival in Tasmanian devils (Sarcophilus harrisii) infected with a transmissible cancer, Molecular ecology, 27(21), 4189-4199



Dear Seb,

Thanks for being so patient with our sass and questions and for making our week so enjoyable - we learnt a heap and had an awesome time!

Rachel (Queen of the Gutes) & Jordann (the perfect one)

PS - Bonne Chance dans votre PhD!

"Nala"
2016